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Seattle, Washington

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Fishery Bulletin

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SCIENTIFIC EDITOR, *Fishery Bulletin*

Dr. Andrew E. Dizon
Southwest Fisheries Center La Jolla Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, CA 92038

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HARBOR PORPOISE, *PHOCOENA PHOCOENA*, ABUNDANCE ESTIMATION FOR CALIFORNIA, OREGON, AND WASHINGTON: I. SHIP SURVEYS

JAY BARLOW[1]

ABSTRACT

The density and total population size of harbor porpoise along the coasts of California, Oregon, and Washington are estimated from ship surveys using line transect methods. Surveys were completed between September 1984 and May 1986 using teams of 3–5 observers. Data include 852 porpoise groups sighted during 6,590 km of transects. Sighting rates varied more due to effects of sea state than due to the presence of rain, fog, or sun glare. Experiments using additional observers indicate that approximately 22% of trackline groups were missed by a team of 5 observers. Harbor porpoise density is calculated from transects along the 18 m isobath and is extrapolated to other depth zones based on a model of porpoise abundance as a function of depth. Total population size is estimated as 45,713 (SE = 7,865) animals.

Approximately 200–300 harbor porpoise are taken annually in central California set net fisheries (Diamond and Hanan[2]; Hanan, et al.[3]). Little is known about porpoise abundance in this area. Dohl et al.[4] estimated that 1,600–3,000 porpoise reside in central and northern California based on their aerial surveys of coastal cetaceans. However, because harbor porpoise are frequently missed in aerial surveys (Kraus et al. 1983), this estimate is probably low. More information is needed on abundance, distribution, and population structure to determine the significance of harbor porpoise mortality in set nets.

Beginning in 1984, the National Marine Fisheries Service (NMFS) has conducted ship and aerial surveys of harbor porpoise abundance in California, Oregon, and Washington. This report presents results from four ship surveys. Results of the aerial surveys are presented by Barlow et al. (1988).

Porpoise density is estimated from survey data using line transect models (Burnham et al. 1980). Total abundance is estimated by extrapolating from density observed along transect lines to the entire area inhabited. Abundance in offshore regions is based on a model of porpoise density as a function of water depth. In addition to abundance estimation, survey data are used to examine the effect of environmental conditions on sighting efficiency and the possibility of temporal changes in harbor porpoise distribution.

METHODS

Ship Survey Methods

Surveys were conducted from two National Oceanic and Atmospheric Administration (NOAA) research vessels, the 52 m RV *David Starr Jordan* (Surveys 1, 3, and 4) and the 54 m RV *McArthur* (Survey 2)[5]. Both vessels were of similar design with viewing stations located on top of the pilothouse (viewing height was approximately 10 m above sea surface). Transect lines followed as close as possible to the 18 m isobath (roughly 2–4 km from the coast), although the actual depth along the transect varied from approximately 15–45 m, depending on the presence of local navigational hazards. The areas

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[2]Diamond, S. L., and D. A. Hanan. 1986. An estimate of harbor porpoise mortality in California set net fisheries: April 1, 1983 through May 31, 1984. Adm. Rep. SWR-86-15, 40 p. Available from National Marine Fisheries Service, Southwest Region, 300 S. Ferry Street, Terminal Island, CA 90731.

[3]Hanan, D. A., S. L. Diamond, and J. P. Scholl. 1986. An estimate of harbor porpoise mortality in California net fisheries April 1, 1984 through March 31, 1985. Adm. Rep. SWR-86-16, 38 p. Available from National Marine Fisheries Service, Southwest Region, 300 S. Ferry Street, Terminal Island, CA 90731.

[4]Dohl, T. P., R. C. Guess, M. L. Duman, R. C. Helm. 1983. Cetaceans of central and northern California, 1980–83: status, abundance, and distribution. Report prepared for U.S. Minerals Management Service, Contract #14-12-0001-29090, 284 p.

[5]Cruise reports available from the Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038.

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surveyed are shown in Figure 1. Survey design varied among the four trips:

Surveys 1 and 3 were in September 1984 and 1985, respectively. Both were designed to survey harbor porpoise density and abundance from Point Conception, CA to Cape Flattery, WA. An attempt was made to survey the entire coastline on each of these cruises, but several sections of the coast were missed (Fig. 1) because of fog and heavy weather. Five observation positions were used on these two surveys.

Survey 2 was from 24 January to 9 February 1985 and was primarily designed to examine seasonal changes in harbor porpoise distribution between Point Conception, CA and Cape Flattery, WA. Data from this cruise were not used for density or abundance estimation.

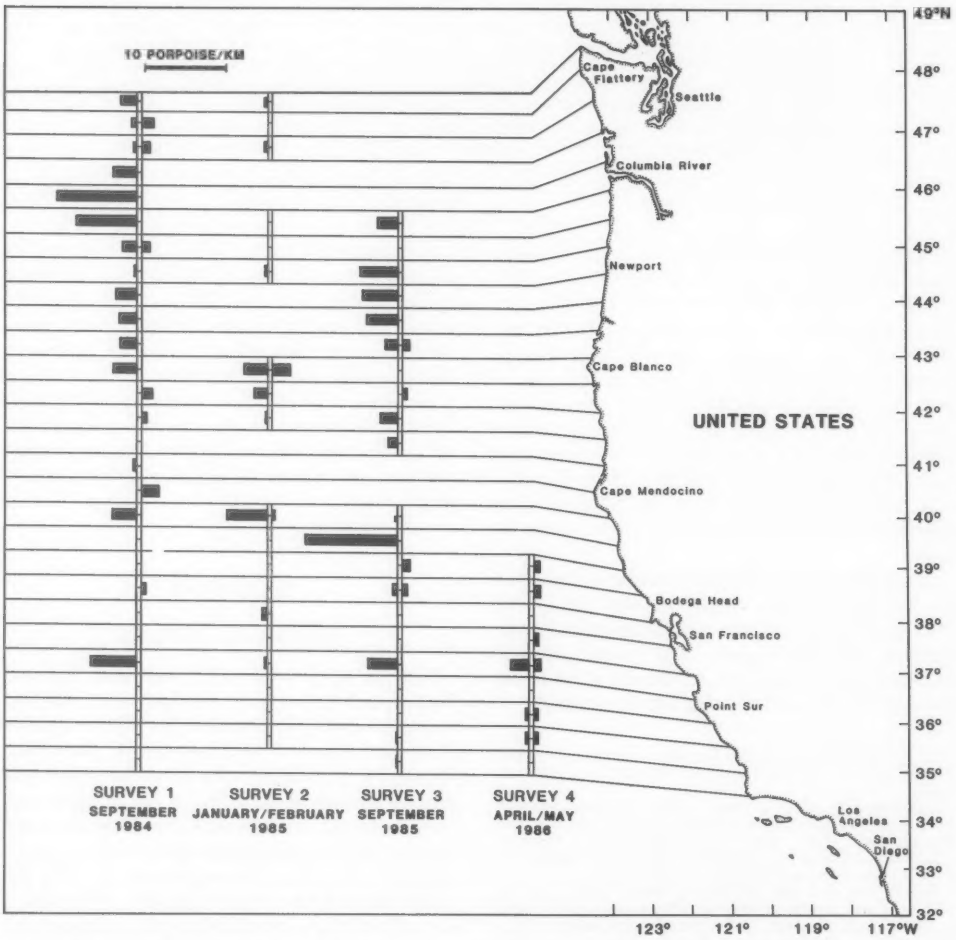

FIGURE 1.—Relative sightings per kilometer based on 30-minute latitudinal strata. Lines parallel to the coast indicate areas that were surveyed. Histograms indicate relative numbers of harbor porpoise seen per kilometer of transect, with bars to the left indicating relative numbers in calm seas (Beaufort 0, 1, and 2) and bars to the right indicating relative number in rough seas (Beaufort 3, 4, and 5).

Survey 4 was from 24 April to 5 May 1986 and was designed to investigate factors which affect harbor porpoise density estimation. The surveys concentrated on several areas of high porpoise density in central California. The vessel's activities were coordinated with a helicopter to gather information on the avoidance of the ship by harbor porpoise. Experiments were also conducted on survey 4 to determine whether an independent team of 3 observers would sight any porpoise that were missed by the primary team of 5 observers. Data from this survey were not used for density or abundance estimation.

Typically, 8–10 observers were used on each survey, with a rested observer starting every half hour and rotating through 5 primary observation positions at half-hour intervals. The 5 positions consisted of port and starboard inboard observers, port and starboard outboard observers, and a recorder positioned amidship. The inboard observers searched with 7 power (7×) binoculars from straight ahead to 90° (survey 1) or to 45° (surveys 2, 3, and 4) on their respective sides of the vessel. On survey 1 the outboard observers searched with 25×, pedestal-mounted binoculars. Although sightings could be made at great distances from the vessel using the 25× binoculars, these distant sightings contributed little to the estimation of trackline density, and use of 25× binoculars was discontinued. On subsequent surveys, both the inboard and outboard observers used 7× binoculars. The outboard observers searched from straight ahead to 90° on their respective sides of the vessel. The recorder searched in the immediate vicinity of the ship using unaided eyes and (intermittently) 7× binoculars.

On survey 2, only 3 observation positions were used from Point Conception to Point Sur, CA and from Point Reyes, CA to Cape Flattery, WA. When effort was reduced to 3 observers, the inside observation positions were eliminated.

On survey 4, a second team of 3 observers was added to monitor the effectiveness of the principal team. This monitor team searched using unaided eyes and (intermittently) 7× binoculars from the pilothouse deck (viewing height approximately 7 m from sea surface). The principal team and the monitor team did not communicate sighting information, and independent records were kept.

Data were noted by the recorder on data coding forms. Data on search effort included the beginning and ending times and positions for continuous legs of effort, the ship's heading and speed, personal identification codes for the observers, sea surface temperature, water depth, Beaufort sea state, sun position relative to the ship, and codes indicating the presence of rain or fog within 5 km. The ship position was determined from a Loran navigational system or by triangulation using coastal landmarks and dead reckoning. Ship speed was recorded directly from the Omega/Loran system or was calculated based on time and distance traveled between successive position fixes along straight transect lines. Water depth was measured using a 38 kHz acoustic depth sounder.

Data for sightings consisted of the above elements, plus estimated group size, distance to shore, an estimate of the angle between the trackline of the ship and the group, and an estimate of the distance from the ship to the group. Group size refers to all the individuals associated with a sighting event. In most cases, groups were closely associated individuals that surfaced together (mean = 2.92, median = 2.0). In two cases (Point Arena and Monterey Bay, CA), groups consisted of 50–80 loosely associated individuals that were organized in subgroups of 4–10). Group size was estimated and recorded independently by each observer; the mean of these estimates was used in subsequent analyses. The angle from the trackline to the porpoise was estimated visually with the aid of a pelorus mounted in front of the observer stations, or, when 25× binoculars were used, from a calibrated collar on the pedestal mount. On surveys 1 and 2, distances to harbor porpoise were estimated visually using the radar distance-to-shore as a reference, or, when 25× binoculars were used, distances were estimated using calibrated reticles in the oculars. On surveys 3 and 4, distances were estimated using calibrated reticles in the oculars of 7× binoculars. Data were also collected on the porpoises' direction of travel relative to the ship.

The length of a transect was estimated as the product of ship speed and elapsed time. To stratify density estimates by sea state, rain, and fog, the effort record was divided into segments during which the sea state, rain, and fog codes did not change.

In five areas, information was collected on variation in harbor porpoise density with water depth. During survey 3, three sections of the coast were surveyed intensively (Fort Bragg to Cape Vizcaino, CA; Cape Blanco to Coquille Point, OR; and Cape Lookout to Tillamook Head, OR), with transect lines following the 18, 56, 92, and 185 m isobaths. On survey 4, the 18 and 46 m isobaths were surveyed in Monterey Bay, CA and in the vicinity of the Russian River, CA. These data formed the basis of a model (below) to extrapolate porpoise density from

the usual transect lines (along the 18 m isobath) to deeper waters.

Helicopter Observations

During survey 4, a Hughes 500-D helicopter was used to collect information on harbor porpoise behavior in response to the survey ship. The helicopter flew approximately 10 km ahead of the vessel, and 3 observers in the helicopter looked for harbor porpoise. Once a group of harbor porpoise was sighted, the helicopter hovered at 200–300 m while observers made behavioral observations and periodically recorded the helicopter's position using an on-board Loran system. Fluorescein dye packages were dropped in the water to allow the helicopter to maintain its position when harbor porpoise were diving. Radio communication was maintained with personnel on the ship who also kept records of the helicopter position using radar distances and bearings based on returns from an X-band radar transponder in the helicopter. The ship changed course, when necessary, to ensure that it passed in close proximity to the porpoise that were being observed. Porpoise observers on the ship were not aware of the helicopter's activities and were not told of sightings made by the helicopter observers (although they were able to see dye patches in some cases). Behavioral observations from the helicopter included time spent at the surface, time spent diving, and direction of porpoise movement.

Density Estimation

Line transect methods were used to estimate the density of harbor porpoise from sightings. The assumptions of these methods are considered in detail in the discussion. The usual formula for estimating density (D) based on line transect surveys of small cetaceans is given by

$$D = \frac{f(0) \cdot n \cdot G}{2 \cdot L} \qquad (1)$$

where $f(0)$ = the probability density function for sightings evaluated at zero perpendicular distance,
n = number of sightings of groups,
G = average group size calculated as the total number of individuals in all groups divided by the number of groups ($\Sigma N/n$), and
L = length of the transect.

(Holt and Powers 1982; Hammond and Laake 1983; Holt in press). I did not use mean group size explicitly in abundance estimation, and density of harbor porpoise individuals, D, was estimated as

$$D = f(0) \cdot (R/2) \qquad (2)$$

where R = the number of individuals seen per length of transect ($\Sigma N/L$).

Equation (2) is functionally equivalent to Equation (1), but it simplifies variance estimation. Typically when using Equation (1), variances (and possibly covariances) must be estimated for $f(0)$, G, and n. Using Equation (2), variances are needed only for $f(0)$ and R, and covariance between mean group size and number of groups is handled implicitly. Sighting distributions appear to be independent of group size, G, (Results section), hence no adjustments were made to $f(0)$ for group size bias.

The parameter $f(0)$ is, in effect, a measure of sighting efficiency and should not vary with porpoise abundance. Sighting efficiency is, however, likely to change with sighting conditions, such as Beaufort sea state. Given these expectations and because relatively large sample sizes are needed to estimate $f(0)$ accurately, values for $f(0)$ were estimated for each survey by pooling all sightings within defined sea state categories. In order to estimate density on a finer scale, estimates of R were stratified by geographic region and multiplied by the pooled estimate of $f(0)$.

The sighting probability density function evaluated at zero distance, $f(0)$, was determined empirically by fitting curves to the frequency distribution of sightings as a function of perpendicular distance from the trackline (Burnham and Anderson 1976). Differences in distributions of perpendicular distance were tested using the Kolmogorov-Smirnov 2-sample test. To avoid bias due to rounding error, angle and radial distance data were "smeared" (Butterworth 1982; Hammond and Laake 1983). Angles were smeared by adding a uniformly distributed random number between $-5°$ and $+5°$ to angle estimates. Radial distances were smeared by adding a uniformly distributed random number between 0.2 and $+0.2$ times the estimated distance. These smearing levels were based on the degree of rounding that was apparent from the data (Barlow[6]).

[6]Barlow, J. 1987. Abundance estimation for harbor porpoise (*Phocoena phocoena*) based on ship surveys along the coasts of California, Oregon, and Washington. Adm. Rep. LJ-87-05.

Several models were investigated for estimating $f(0)$ from sighting distributions. The FORTRAN program Transect (Laake et al. 1979) was used to fit 2-, 3-, 4-, and 5-parameter Fourier series and 2-parameter exponential power series models. The FORTRAN programs Hazard and Hermite (S. Buckland[7]) were used to fit the 2-parameter hazard rate model (constrained such that parameter $P > 2$, Buckland 1985) and the 1-, 2-, 3-, and 4-parameter Hermite polynomial model (Buckland 1985). Of these models, the 2-parameter hazard rate model was selected based on its ability to fit the observed distributions and its lack of dependence on grouping criteria (Buckland 1985).

Perpendicular distances were grouped into strata, the size of which increased with perpendicular distance: 0–25 m, 25–50 m, 50–100 m, 100–200 m, 200–400 m, 400–800 m, 800–1,600 m, and 1,600–3,200 m. Several alternative groupings were investigated, and the choice of cutpoints made very little difference in estimates of $f(0)$. The above strata (increasing with distance) gave lower variances in $f(0)$ than when each stratum was of equal size (possibly because the hazard rate model assumes a distinct shoulder in the sighting distribution, and that shoulder is lost if the first distance strata are large).

No established criteria exist for choosing an appropriate perpendicular distance at which to truncate sighting distributions. Burnham et al. (1980) recommend that no more than 1–3% of sightings be eliminated by truncation. Using this recommendation, models were not able to adequately fit the observed sighting distributions. In this report, truncation distance was chosen in four ad hoc steps: 1) The hazard rate model was fit to perpendicular distance data truncated at distances of 400, 800, 1,600, and 3,200 m. 2) Truncation distances were identified which gave acceptable χ^2 values ($P > 0.1$). 3) Of the acceptable truncation distances, the standard error in $f(0)$ was estimated empirically by randomly drawing 10 samples (of the same size as the original sample) from the observed distribution of perpendicular distances and by calculating the standard deviation of $f(0)$ estimated from each random sample. 4) Truncation distances were chosen as those which gave the lowest coefficient of variation in $f(0)$.

Variance in R, the number of porpoise seen per kilometer, was estimated using jackknife statistics (Efron 1982). Jackknife estimates were calculated by first estimating the value of R using all data. The value, R_k, was again estimated excluding the kth segment of search effort. This process was repeated for each effort segment. To ensure that each kth segment was of equivalent length, effort segments with the same sea state, rain, and fog codes were combined in a linear array and were then divided into 10 segments of approximately equal length. The variance in the estimate of R was calculated as

$$s^2 = \frac{9}{10} \cdot \sum_{k=1}^{10} (R_k - \bar{R})^2 \qquad (3)$$

The variance of D was estimated using the Goodman (1960) product variance formula (assuming no covariance) using this jackknife variance for R and the above Monte Carlo variance for $f(0)$.

Fraction of Missed Animals

On survey 4, a second, independent team of 3 observers were used to estimate the fraction of harbor porpoise that are missed by the primary team of 5 observers. The fraction of missed animals in a sighting survey is analogous to the fraction of unmarked animals in a mark/recapture experiment (Pollock and Kendall 1987). This fraction was estimated using the Chapman (1951) modification of the Petersen (or Lincoln) index method (Pollock and Kendall 1987). Confidence limits were estimated using Adams' (1951) method, which assumes a binomial sampling distribution. Standard error was estimated using standard binomial formulas.

Abundance Estimation

A model was used to estimate the number of harbor porpoise along the entire coastline based on the density that was observed along the 18 m isobath. In shallow areas, such as the Bering Sea and Georges Bank, harbor porpoise are found a considerable distance from land (Gaskin 1984), hence offshore distribution is better modelled as a function of depth than as a function of distance from shore. (Although harbor porpoise are also found in very deep water in fjords and inland waterways of Alaska [Taylor and Dawson 1984], this represents a special case that is not applicable to coastal waters considered here.) The model used to estimate abundance was based on data collected on surveys 3 and 4 and on data from a ship surveys by La Barr and

Avail. from Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038.

[7]S. Buckland, Inter-American Tropical Tuna Commission, P.O. Box 271, La Jolla, CA 92038, pers. commun. July 1986.

Ainley[8] and Szczepaniak[9] in central California. The number of harbor porpoise seen per kilometer of transect was taken as an index of relative density along each isobath. A simple descriptive model was then constructed to give relative density as a function of water depth.

Fifteen depth strata were used in abundance estimation: 0–10, 10–20, 20–30, . . . , and 140–150 m. The surface area within the strata was calculated from digitized bathymetric data. Kelp beds were assumed to be unsuitable as harbor porpoise habitat; hence, kelp bed area was subtracted from the total area within the 0–10 m stratum. Kelp bed areas for the entire west coast were taken from Crandall (1915). More recent estimates for limited areas in central California are in good agreement with these previous values (G. Van Blaricom[10]).

For each of 15 depth strata, the abundance of harbor porpoise was estimated as the product of their density along the survey line (the 18 m isobath), the density in that depth strata relative to that along the survey line, the surface area included within that depth strata, and the inverse of the estimated fraction of trackline animals that were seen. Since survey effort and harbor porpoise density both varied geographically, abundance estimates were made for each of 8 geographic regions (Fig. 2). Areas within the depth strata were estimated from NOAA bathymetric data. The estimate of total abundance along the coast, N_T, is therefore given by

$$N_T = \frac{1}{F} \cdot \sum_{j=1}^{8} D_j \sum_{k=1}^{15} (I_k \cdot A_{j,k}) \qquad (4)$$

where D_j = density of individuals observed on the transect line in the jth geographic strata,

I_k = ratio of density in depth strata k to that on transect line (see Figure 4),

$A_{j,k}$ = area in geographic region j and depth strata k, and

F = the estimated fraction of trackline animals seen by the usual team of 5 observers.

Equation (4) was applied independently to the different surveys and, within surveys, to different sea state strata. When combining estimates from different sea states or different cruises, abundance was calculated as the mean of the densities in each of the stratum, weighted by the length of the transect line within that stratum.

In estimating standard error for total abundance, variances of products were calculated using the Goodman (1960) product variance formula, and variances of ratios were estimated using a Taylor approximation (Yates 1953, p. 198). Area was assumed to be known without error. Statistical error in the indices of abundance for the depth strata could not be estimated given the paucity of available information. To account for uncertainty in the model of depth distribution, three versions of the model are proposed to span a range of possibilities.

RESULTS

On the four surveys, 852 groups of harbor porpoise were sighted (an estimated 1,818 individuals). A distance of 6,590 km was surveyed during 56 days. The number of sightings per kilometer surveyed varied geographically and these geographic patterns appeared to change appreciably between cruises (Fig. 1).

Sighting Distributions

The number of sightings on the inshore and offshore sides of the vessels were approximately equivalent (383 and 392, respectively). The cumulative distributions of perpendicular sighting distances were not significantly different for these two sides ($P = 0.06$). Therefore, sighting distributions were assumed to be symmetrically distributed about the trackline, and the distributions of perpendicular sighting distances from both sides of the vessel were pooled for subsequent analyses.

The distributions of perpendicular sighting distances for the first three surveys were significantly different from one another ($P < 0.01$ for all). This was probably the result of the modifications in survey methods between these cruises. Surveys 3 and 4 used the same methods, and sighting distributions were not significantly different ($P = 0.39$). Given that changes in methods result in differences in sighting distributions, all surveys were treated separately in subsequent analyses.

Distributions of perpendicular distance were not significantly different between individuals sighted

[8]LaBarr, M. S., and D. G. Ainley. 1985. Depth distribution of harbor porpoise off central California: A report of cruises in April and May–June 1985. Report to U.S. National Marine Fisheries Service, Northwest and Alaska Fishery Center, 7600 Sand Point Way N.E., Seattle, WA. Contract No. 41-USC252.

[9]Szczepaniak, I. D. 1987. Abundance and distribution of harbor porpoise (*Phocoena phocoena*) in the Gulf of the Farallones National Marine Sanctuary. Contract report prepared for National Park Service, Point Reyes National Seashore, Point Reyes, CA 94956.

[10]G. Van Blaricom, U.S. Fish and Wildlife Service, University of California, Santa Cruz, CA 93106, pers. commun. August 1986.

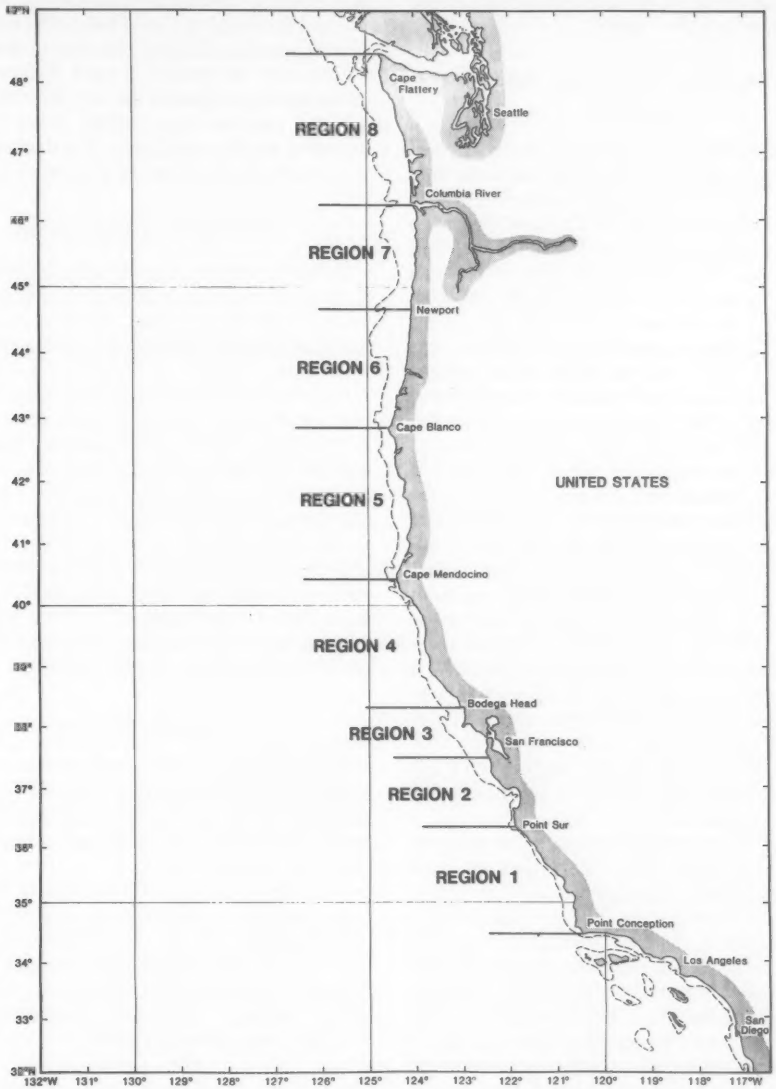

FIGURE 2.—Geographic regions used as strata in abundance estimation. Broken line indicates the 200 m isobath and delineates likely harbor porpoise habitat.

alone (group size of 1) and larger groups (group size of 3 and greater) (P = 0.56).

Environmental Conditions Affecting Sightings

Sighting efficiency was not significantly affected by rain, fog, or sun glare. Rain/fog conditions were considered "poor" if rain or fog were present within 5 km of the vessel and "good" if neither were present. The distributions of perpendicular sighting distances were not significantly different between these two strata (P = 0.32, 0.44, 0.78, and 0.64, respectively, for surveys 1, 2, 3, and 4), and the number of porpoise per kilometer surveyed was higher in the "poor" category for two of the surveys. Sun glare from the water's surface was considered to contribute to "poor" sighting conditions if the sun was within 45° of the trackline in front of the ship. Conditions were considered "good" when the sun was in other positions or was obscured by clouds. As with rain/fog conditions, the distributions of perpendicular sighting distances were not significantly different between these "good" and "poor" sun glare categories (P = 0.87, 0.47, 0.30, and 0.55, respectively, for surveys 1, 2, 3, and 4). The number of harbor porpoise per kilometer surveyed were slightly higher in the poor category for three of the surveys. In paired comparisons when glare was present on only one side of the bow, approximately equal numbers of sightings were made on the sides with and without glare (60 vs. 59, respectively). All categories of rain, fog, and glare are included in subsequent analyses.

Sea state did have a significant effect on porpoise sightings. Sea state was categorized as calm (without white-caps, Beaufort sea states 0, 1, and 2) or rough (with white-caps, Beaufort sea states 3, 4, and 5) following the classification used by Holt and Cologne (1987). Distributions of perpendicular distances were not significantly different between these categories for any of the surveys ($P > 0.05$); however for all surveys combined, the number of harbor porpoise detected per kilometer was much lower during rough seas (0.32 km^{-1}) than during calm seas (1.22 km^{-1}). There were insufficient sightings to estimate density for rough seas separately; therefore, rough sea data were excluded in subsequent analyses. For all three surveys, the numbers of harbor porpoise detected per kilometer was higher at Beaufort 0 & 1 than at Beaufort 2, and for survey 3, the distributions of perpendicular sighting distance were significantly different between these categories (P = 0.03). Porpoise density is, therefore, estimated separately for Beaufort 0 & 1 and for Beaufort 2 conditions. (For comparison, harbor porpoise abundance was also estimated pooling Beaufort sea states 0, 1, and 2. Estimated abundance was approximately the same by both methods, but the variance was slightly lower using the stratified sea state categories. For this reason, only the stratified estimates are presented here.)

Helicopter Observations

Helicopter observation of the behavior of harbor porpoise in response to the survey ship were made on only 6 groups of animals. Plots of vessel tracks and movements of the groups are given in the cruise report (see footnote 5). Only in one case was a distinct behavioral change noted in response to the ship. In that case, when the vessel was within 800 m, the group moved rapidly, perpendicular to the path of the vessel and then parallel to and in the opposite direction of the vessel. Observers on the ship saw this harbor porpoise group as they moved rapidly out of the path of the vessel. Observers on the ship also saw 2 of the other 5 groups. Although this sample of behavior is small, movement in response to the survey vessel appeared limited to within 1 km of the vessel and, when it occurred, animals did not travel far from their original positions.

Porpoise Density

The probability density distributions of perpendicular sighting distances are shown in Figure 3 for surveys 1 and 3 and for Beaufort sea states 0 & 1 and 2. The hazard rate model gave acceptable fits for all sighting distributions ($P > 0.1$) when the truncation criteria was set at 400 m (Table 1). For survey 1, the optimum truncation points were chosen as 400 m for Beaufort 0 & 1 and 800 m for Beaufort 2; for survey 3, this distance was 400 m for both Beaufort sea state categories. The fits of these models are shown in Figure 3. Estimates of density and standard errors are given in Table 2.

Depth Distribution Model

The model of harbor porpoise depth distribution was based on the relative densities of harbor porpoise at different water depths. Ship survey data were pooled into five depth ranges: 18–37 m (10–20 fathoms), 37–55 m (20–30 fathoms), 55–73 m (30–40 fathoms), 73–91 m (40–50 fathoms), and 91–110 m (50–60 fathoms). Ship surveys are generally not practical inshore of the 18 m isobath, but estimates

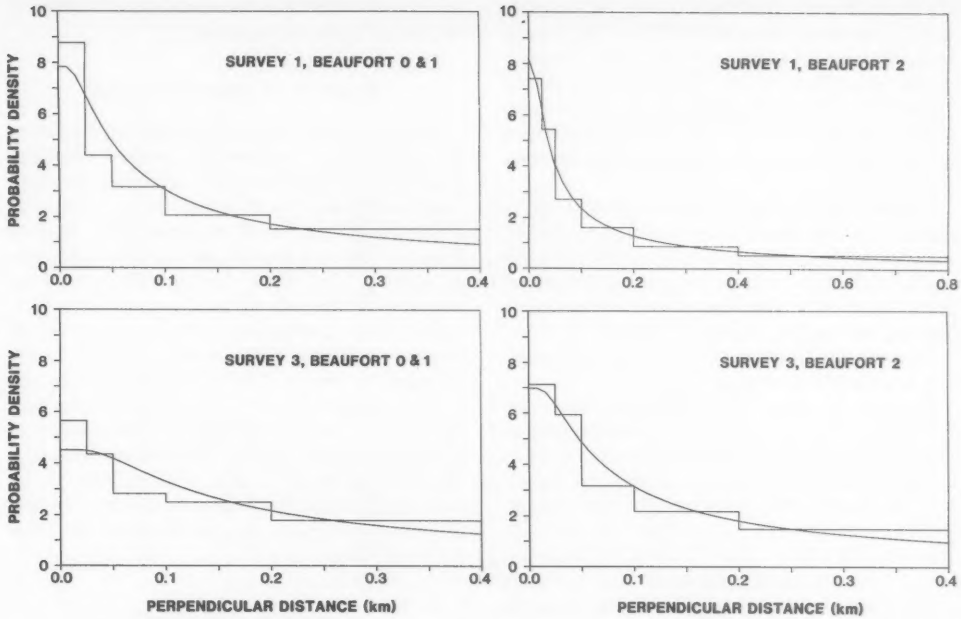
SURVEY 1, BEAUFORT 0 & 1
SURVEY 1, BEAUFORT 2
SURVEY 3, BEAUFORT 0 & 1
SURVEY 3, BEAUFORT 2
PROBABILITY DENSITY
PERPENDICULAR DISTANCE (km)

FIGURE 3.—Probability density distributions for perpendicular sighting distances. Histograms indicate observed distributions, and solid lines indicate the best fit of the hazard rate model to these data.

TABLE 1.—Estimated values of the probability density functions evaluated at zero perpendicular distance, $f(0)$. Estimates are based on the hazard rate model and were made for truncation distances of 400, 800, 1,600, and 3,200 m. Estimates are given only if the model gave an acceptable fit to the data ($P > 0.1$). Asterisks indicate $f(0)$ values with the lowest coefficient of variation (parentheses).

Survey	Beaufort sea state	Truncation distance 400 m	800 m	1,600 m	3,200 m
1	0 & 1	7.85 * (0.23)	5.31 (0.29)	4.31 (0.24)	— —
1	2	10.48 (0.59)	8.15 * (0.21)	7.09 (0.33)	5.78 (0.51)
3	0 & 1	4.51 * (0.22)	3.10 (0.66)	2.69 (0.31)	— —
3	2	6.97 * (0.19)	— —	— —	— —

from aerial surveys (Barlow et al. 1988) show roughly equal density at 0.61 and 1.85 km from the shore (the latter corresponding approximately to the 18 m isobath). Relative density from ship surveys was measured in the number of sightings per kilometer of searching effort. Relative densities at

TABLE 2.—Density estimates, D, for harbor porpoise (km^{-2}) along the 18 m isobath in each of eight geographic strata. Density was calculated per Equation (2), using estimates of $f(0)$ (Table 1) which had the lowest coefficients of variation. Values are not adjusted for missed animals. Standard errors are in parentheses.

Geographic region	Survey 1 Beaufort 0 & 1	Survey 1 Beaufort 2	Survey 3 Beaufort 0 & 1	Survey 3 Beaufort 2	Pooled estimates
1	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)	0.04 (0.02)
2	1.1 (1.0)	0.0 (0.0)	0.6 (0.5)	0.1 (0.1)	0.51 (0.30)
3	—	0.0 (0.0)	0.1 (0.1)	0.0 (0.0)	0.03 (0.03)
4	—	2.5 (1.0)	0.0 (0.1)	6.7 (7.2)	2.83 (1.69)
5	—	2.1 (1.3)	0.8 (0.6)	0.6 (0.3)	0.91 (0.32)
6	1.4 (0.8)	2.0 (0.6)	2.5 (0.8)	2.6 (0.9)	2.22 (0.40)
7	7.9 (3.4)	0.8 (0.6)	2.5 (0.6)	1.3 (0.7)	2.64 (0.78)
8	1.8 (0.8)	0.0 (0.0)	—	—	1.09 (0.45)
Total	2.5 (1.1)	1.3 (0.6)	0.8 (0.4)	1.2 (0.5)	1.33 (0.30)

18–37 m show no consistent relationship to those at 37–55 m or 55–73 m (Table 3), but on average these appear to be approximately equal. Relative densities at 18–37 m are, however, consistently higher than densities at 73–110 m in all areas (Table 3). A total of 236 km were searched in waters deeper than 110 m and no harbor porpoise were seen.

Despite high variability in patterns of depth distribution and lack of ship coverage in shallow waters, some generalizations can be made about the depth distribution of harbor porpoise along the west coast. The relative abundance of harbor porpoise appears to be roughly constant from shore to 55 m, to be markedly lower at 73–110 m, and to be very low in waters deeper than 110 m.

Based on the above relationships, I propose the following preliminary model for the depth distribution of harbor porpoise along the coasts of California, Oregon, and Washington: constant abundance from the coast to the 80 m isobath, linearly decreasing abundance from the 80–120 m isobaths, and zero abundance in waters deeper than 120 m (Fig. 4a). Because considerable uncertainty exists in this model, I propose two alternative models (Fig. 4b, c). Alternative models b and c are less likely than the primary model given because both conflict with some of the available data. The alternative models do, however, encompass the likely range of relative density values and provide a means to evaluate the sensitivity of the abundance estimate to different models of depth distribution.

Fraction of Missed Animals

The experiment on survey 4 indicates that some trackline groups were seen by 1 group of observers and were missed by the other. A total of 103 sightings was made by both teams, 33 of which were estimated to be within 100 m perpendicular distance from the transect line. Of the 103 total sightings, 85 were detected only by the 5 principal observers, 6 were detected only by the 3 monitor observers, and 12 were detected by both teams. Of the 33 trackline sightings, 20 were detected only by the principal observers, 3 were detected only by the monitor observers, and 10 were detected by both teams. The Petersen estimate of the fraction of trackline porpoise seen by the primary team of 5 observers is thus 0.780 (SE = 0.117, 95% C.L. = 0.45–0.95). This indicates that approximately 22% of trackline sightings are missed by the principal teams of 5 observers.

Porpoise Abundance

Estimates of porpoise abundance in each of the eight geographic strata are given in Table 4 for the primary model of offshore distribution. Independent estimates are given for survey 1 and for survey 3

TABLE 3.—Relative harbor porpoise abundance observed within the specified depth ranges at a variety of study sites. Relative abundance is measured as number of porpoise sightings made per kilometer. Numbers in parentheses indicate kilometers surveyed.

Location	Depth range				
	18–37 m	37–55 m	55–73 m	73–91 m	91–110 m
Central California[1]	0.02 (89)	0.08 (172)	0.03 (403)	0.03 (279)	0.01 (166)
Gulf of the Farallones, CA[2]	0.29 (181)	0.00 (159)	0.30 (133)	0.00 (7)	0.00 (7)
Fort Bragg, CA	0.05 (41)	—	0.05 (43)	—	0.03 (35)
Coquille Pt, OR	0.24 (43)	—	0.35 (52)	—	0.08 (50)
Tillamook Head, OR	0.50 (57)	—	0.12 (52)	—	0.00 (17)
Monterey Bay, CA	0.46 (220)	0.29 (76)	—	—	—
Russian River, CA	0.00 (26)	0.30 (33)	—	—	—

[1]Data taken from LaBarr and Ainley (see text footnote 8) assuming an average survey speed of 9 knots.

[2]Data taken from Szczepaniak (see text footnote 9) assuming an average survey speed of 9 knots.

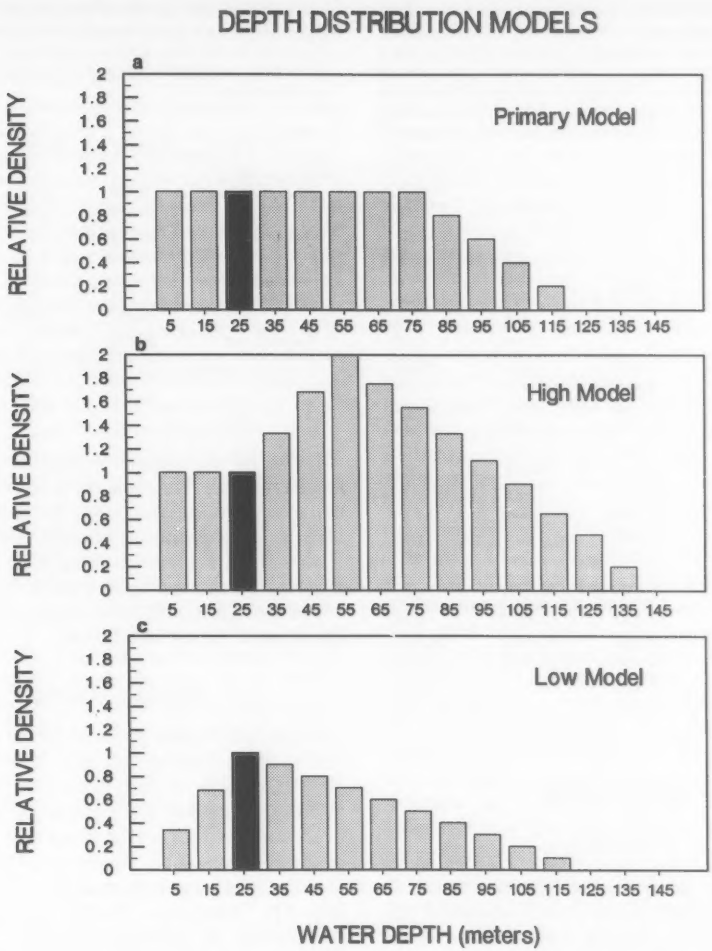

FIGURE 4.—Proposed models for the depth distribution of harbor porpoise expressed as relative densities, I_k, within 10 m depth intervals. Density at 20–30 m is assumed to be known and is given a relative value of 1. Figures represent a) a primary model of offshore distribution, b) a high estimate of offshore range, and c) a low estimate.

in each area. Both surveys show similar patterns, with higher abundances in the northern strata (4–8) and very low abundance in strata 1 and 3. Despite similar patterns, differences between the paired estimates are in some cases, large and statistically significant (t-tests, $P < 0.05$). Because region 8 was not covered on the third survey, it is not possible to compare estimates of total abundance for the entire coast between surveys. The total abundances for regions 1–7 (Point Conception to the Columbia River) are 46,550 (SE = 10,932) animals and 32,029 (SE = 10,906) animals for surveys 1 and 3, respectively. The difference between these estimates is not statistically significant (t-test, $P > 0.05$). Pooling the results of the two surveys, the estimate of harbor porpoise abundance between Point Conception and Cape Flattery in September of 1984 and 1985 is 45,713 (SE = 7,865) animals (Table 4). The same estimate using the alternate models of offshore distribution ranges from 28,769 to 78,019 (Table 5).

TABLE 4.—Estimated abundance of harbor porpoise in each of the eight geographic strata based on the primary model of offshore distribution. Estimates for Beaufort 0 & 1 and for Beaufort 2 were computed separately and then averaged, weighting by transect length. Pooled estimates for the eight strata were obtained as an average of the two surveys, weighting by transect length. All estimates are adjusted for missed animals. Standard errors are in parentheses.

Geographic region	Survey 1	Survey 3	Pooled estimates
1	0	126 (68)	96 (52)
2	2,401 (2,180)	932 (646)	1,459 (885)
3	0	153 (158)	112 (116)
4	6,909 (2,959)	9,096 (9,855)	7,909 (4,784)
5	11,245 (6,943)	3,296 (1,410)	4,806 (1,745)
6	9,061 (2,724)	12,786 (3,676)	11,107 (2,363)
7	16,934 (7,097)	5,641 (2,424)	10,416 (3,311)
8	9,808 (4,311)	—	9,808 (4,311)
Totals			
Regions 1–3	2,401 (2,180)	1,210 (669)	1,667 (895)
Regions 1–7	46,550 (10,932)	32,029 (10,906)	35,904 (6,578)
Regions 1–8	56,358 (11,751)	—	45,713 (7,865)

TABLE 5.—Estimated abundance of harbor porpoise in central California (regions 1–3) and along the entire coast (regions 1–8) based on two alternate models of offshore distribution. All estimates are adjusted for missed animals. Standard errors are in parentheses.

	Survey 1	Survey 3	Pooled estimates
Alternate Model b			
Regions 1–3	3,966 (3,602)	1,986 (1,104)	2,744 (1,478)
Regions 1–8	95,132 (19,515)	—	78,019 (13,356)
Alternate Model c			
Regions 1–3	1,505 (1,367)	770 (421)	1,054 (561)
Regions 1–8	35,736 (7,550)	—	28,769 (4,995)

DISCUSSION

Distribution

Harbor porpoise are not uniformly distributed between Cape Flattery and Point Conception. Although there are no obvious discontinuities within this range, density varies geographically and temporally. The most dramatic temporal changes are between the two September surveys and the January–February survey (Fig. 1). The coasts of Washington and northern Oregon were found to have relatively high densities of harbor porpoise in September, but, despite excellent sighting conditions, very few porpoise were seen there in January. High densities of harbor porpoise were also seen in Monterey Bay on both September cruises and on survey 4 in May. This area was intensively surveyed in February, and few harbor porpoise were seen. As can be seen in Figure 1, adjacent areas tended to have similar densities within a survey. Less consistency is found when the same areas are compared between different surveys.

The apparent changes in distribution could be caused by small changes in depth distributions. The majority of survey effort was along the 18 m isobath. A large fraction of animals could be missed if their depth distribution changed by 10 m or less. More information on depth distributions is needed before the apparent temporal changes in geographic distribution can be interpreted.

Porpoise Density

Estimates of harbor porpoise density ranged from 0.03 to 2.8 animals/km^2 along transect lines in the eight geographic regions (pooled estimates, Table 2). In another study, Szczepaniak (fn. 9) estimated 0–1.9 porpoise/km^2 in four study areas in the Gulf of the Farallones, CA. Taylor and Dawson (1984) found 1.2–5.9 porpoise/km^2 at study sites in Glacier Bay, AK. Flaherty and Stark[11] estimated 0.8–1.6 porpoise/km^2 in Washington Sound. Densities in the present study are therefore within the range of densities found in other areas along the same coast.

Harbor porpoise density was estimated for California, Oregon, and Washington based on aerial surveys that were concurrent with the present study (Barlow et al. 1988). The overall estimate of harbor porpoise density from that study (corrected for missed animals) was 1.79 porpoise/km^2. The overall estimate from the ship survey (1.33 porpoise/km^2) can be corrected for missed animals to yield an estimate of 1.73 porpoise/km^2. Given that the coef-

[11]Flaherty, C., and S. Stark. 1982. Harbor porpoise (*Phocoena phocoena*) assessment in "Washington Sound". Final Report #80-ABA-3584 submitted to National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way, NE, Seattle, WA 98115. 84 p.

ficient of variation in the pooled ship estimates is nearly 25%, these estimates are in very close agreement. However, because the aerial estimates are based only on the small fraction of the coastline that was surveyed under optimal conditions, the ship estimates are probably a better representation of porpoise density for the entire coast.

Of the areas surveyed, harbor porpoise density is highest in northern California and Oregon. The highest density was seen in northern Oregon (region 7) during survey 1. The second highest density was observed in northern California between Bodega Head and Cape Mendocino (region 4) on survey 3.

Two areas in central California (regions 1 and 3) were found to have very low densities. Region 1 includes the Big Sur coastline from Point Conception to Point Sur. This area is characterized by steep depth gradients and hence has little habitat that is suitable for harbor porpoise. Region 1 was relatively well covered, with 378 km of trackline surveyed at Beaufort sea states 0–2. In contrast, region 3 includes the Gulf of the Farallons with its broad coastal shelf within the 100 m isobath. Based on surveys of 764 km, Szczepaniak (fn. 9) estimated 1,033 harbor porpoise are found in the Gulf of the Farallones alone. This is much greater than my estimate of 112 animals in region 3 based on only 175 km of survey effort. Because of his greater amount of search effort in this area, I believe that Szczepaniak's estimates for region 3 are more accurate than mine. Although regions 1 and 3 were both identified as low density areas, more confidence can be placed on this conclusion for region 1 than for region 3.

Abundance

The size and behavioral characteristics of harbor porpoise make estimating their abundance difficult. Harbor porpoise are small, occur in groups of only a few individuals, and surface without conspicuous splashes; their distribution is extremely patchy. Even with 5 observers, the effective path width that can be searched from a ship is <1 km, and that path width decreases very rapidly in rougher sea states. All of these factors contribute to high variability in the abundance estimates presented here. Seasonal and year-to-year changes in the distribution of harbor porpoise may also contribute to the variability seen within geographic strata. These are, however, the best (and, for some regions, the only) estimates of harbor porpoise abundance for the study area.

Although there are no prior estimates for Oregon or Washington coasts, Dohl et al. (fn. 4) estimated harbor porpoise abundance in central and northern California. Their estimates range from 3,000 harbor porpoise in autumn to 1,600 in summer, which correspond (approximately) to the pooled estimate of 11,457 for regions 1–4 based on the present study. There are, however, several problems with the application of their methods to the estimation of harbor porpoise abundance. In a direct comparison with shore counts, Kraus et al. (1983) showed that observers on aircraft saw only 10–20% of harbor porpoise groups. Dohl et al. (fn. 4) did not apply a correction to account for harbor porpoise groups that are submerged at the time the aircraft passed. Also, Dohl et al. did not stratify estimates by distance from shore or depth. Although most of their harbor porpoise sightings were within 0.5 km (0.25 nmi) of shore, their density estimates were extrapolated to an area extending 166 km from the coast. Estimates from the current study are based on better methodology than previous estimates.

In addition to exposed coastal habitats, harbor porpoise are also found in bays along the coasts of California, Oregon, and Washington. Goetz (1983) reported that harbor porpoise are found throughout the year in Humboldt Bay, CA. Harbor porpoise have been seen in San Francisco Bay, but are described as rarely present[12]. Abundance of harbor porpoise in inland waters may, however, vary seasonally (Taylor and Dawson 1984). No estimates exist for the total number of harbor porpoise inhabiting bays. Survey effort in the present study was limited to exposed coastal areas (including Monterey Bay, but excluding San Francisco Bay, Humboldt Bay, Coos Bay, Yaquina Bay, the mouth of the Columbia River, Willapa Bay, and Grays Harbor). If harbor porpoise density in bays were the same as that which was observed along the 18 m isobath, population sizes presented here could be increased by approximately 3.1% to account for porpoise inhabiting 900 km^{-2} (the approximate combined area of Humboldt Bay, Coos Bay, Yaquina Bay, the mouth of the Columbia River, Willapa Bay, and Grays Harbor).

Line Transect Assumptions

Biases in abundance estimates can be an even greater problem than high variability. In the case of estimates presented here, biases could be introduced if the assumptions of line transect sampling

[12]Szczepaniak, I. D., and M. A. Webber. 1985. Status of the harbor porpoise (*Phocoena phocoena*) in the eastern North Pacific, with an emphasis on California. Contract report to the Center for Environmental Education, Washington, D.C., 52 p.

are not met (Burnham et al. 1980; Hammond and Laake 1983). Of these assumptions, the most relevant to this study are 1) the area must be sampled randomly or the animals must be randomly distributed within the area; 2) all groups on the trackline must be detected; and 3) group size must be estimated without error. These assumptions will be addressed below.

To address the first assumption (random distribution), cruise tracks were chosen to systematically cover the coast from Point Conception to Cape Flattery. Because the surveys were designed to cover the entire longshore range of harbor porpoise in this area, randomly placed survey tracks were deemed unnecessary. Although some areas of the coast were missed, these locations were determined by weather and were presumably not correlated with porpoise abundance. Surveys were, however, limited to a very narrow strip along the 18 m isobath. Initially, the choice of this survey track was based on the observation that, in aerial surveys, harbor porpoise were usually found within 0.5 km (0.25 nmi) of the shoreline in California (Dohl et al. fn. 4). The 18 m isobath was simply the shallowest reasonable working depth for the NOAA survey ships. In the course of these surveys, it was found that harbor porpoise are commonly distributed much further from the coast than 0.5 km and that one survey track could not adequately cover their habitat. The offshore distribution of harbor porpoise is not random, but is related to water depth, distance from shore, or both. The model from which I extrapolated density at 18 m to density at other depths was based on a rather limited sample at a few locations along the coast. The assumption of random search in offshore areas was not met. Additional work is required to evaluate the effect of this.

The second assumption is that 100% of the animals in the immediate vicinity of the trackline were detected. Animals near the trackline can be missed because they move away from the path of the ship, because they do not surface within the visual range of the observers, or because the observers fail to detect animals that do surface. Any of these would result in a negative bias and an underestimation of porpoise abundance using line transect methods. These three problems are considered in more detail.

West-coast harbor porpoise are commonly said to avoid vessels (Flaherty and Stark fn. 11; Szczepaniak and Webber fn. 12) and may be missed or not counted in the proper perpendicular distance category for this reason. On the surveys, the majority of harbor porpoise were oriented roughly parallel to the ship at the time they were sighted and were swimming parallel to the ship and in the opposite direction (see footnote 5). This was also observed in one instance from the helicopter; however, in that case the group first moved perpendicular to the path of the ship. These observations indicate that harbor porpoise are reacting to the ship before they are seen by observers. Reaction to and avoidance of the ship does not necessarily mean that estimates of trackline density are biased if animals are detected before they travel an appreciable distance from the trackline. In several instances, harbor porpoise surfaced within 50 m of the ship and directly in its path. These animals appeared startled and quickly moved to avoid the ship. In these cases, the rapid movement of the animals and splashes associated with that movement made the animals more visible to observers. Because avoidance behavior may make harbor porpoise more visible and because the distributions of perpendicular distance show only a single mode (at the origin), vessel avoidance probably does not introduce a large bias in harbor porpoise abundance estimation. More work is needed in this area.

Harbor porpoise near the trackline may also be missed if they either inadvertently or intentionally do not surface within the visual range of the observers. Typical mean dive times for harbor porpoise have been measured as 1.5–2.3 minutes (Glacier Bay, AK; Taylor and Dawson 1984), 1.8 minutes (northern Oregon; B. Taylor[13]), and 0.4–1.4 minutes (Bay of Fundy; Watson and Gaskin 1983). The ships' speed during surveys was approximately 18.5 km/h or 310 m/min; thus, in 2 minutes the ship would travel 620 m. The average distance at which animals were first seen was 704 m from the ship. If individual dive times were appreciably longer than 2 minutes, some trackline individuals would not be detected by observers. In data collected in northern Oregon, 16% of dive times were greater than 2.5 minutes (B. Taylor fn. 13). In addition, harbor porpoise have been reported to increase dive times up to 7 minutes in the presence of boat traffic (Flaherty and Stark fn. 9). (This latter estimate is considerably longer than any other published estimate, and it is possible that those researchers missed one or more surfacings). Helicopter observations in Monterey Bay indicated that porpoise groups did not extend dive times in the presence of the survey vessel (see footnote 5). This area might not be representative, however, because harbor porpoise may

[13]B. Taylor, Department of Biology, University of California, San Diego, CA 92093, pers. commun. August 1986.

be more accustomed to vessel traffic there than along the majority of the coast. It is likely that some harbor porpoise are missed because they do not surface near the vessel; however, it is not possible to quantify this source of bias without additional study.

Trackline animals may be missed even if they do not avoid the ship and do surface within visual range of the observers if their surfacing is not detected. In another study comparing ship surveys to aerial and shore surveys, Kraus et al. (1983) found that observers on ships saw only about 50% of the harbor porpoise in an area. In that study, however, ship observers stood only 2.5 m above the sea surface (versus 10 m in this study), and the estimate of 50% was based on all groups, not just on trackline animals. Based on the experiment using monitor observers in the present study, an estimated 22% of harbor porpoise that surface on the trackline are missed by the usual team of 5 observers. If this is underestimated by some percentage, population size would be underestimated by the same percentage.

The third critical assumption is that group size is estimated without error. In the case of harbor porpoise, group size is small and estimates are typically based on actual counts. For tropical dolphins, which school in groups of several hundreds, the problem of group size estimation is more acute (Holt and Powers 1982; Hammond and Laake 1983). Only in two instances did harbor porpoise group size exceed 20: in Monterey Bay and near Point Arena, both in California. Excluding these two sightings, mean group sizes are 2.05, 2.33, 2.03, and 1.59 for surveys 1, 2, 3, and 4 (respectively); including the two sightings, means are 2.30 and 2.26 for surveys 1 and 3. These values are comparable to other estimates of mean group size for coastal populations of harbor porpoise: 2.2 based on aerial surveys in California (Dohl et al. fn. 4), 2.6 based on ship surveys in the Gulf of the Farallons (Szczepaniak and Webber fn. 12), 2.3 based on shore surveys in northern Oregon (see footnote 5), and 2.75–3.23 based on aerial surveys along California, Oregon, and Washington (Barlow et al. 1988). The consistency of all these estimates from different platforms indicates that group size estimation from ships is not likely to be a major source of bias in abundance estimation.

Variance Estimation

Although the estimates of standard error for abundance and density are very high, these may still be underestimates because the choice of a truncation criterion was based on minimizing variance and because all possible sources of sampling errors were not considered. The model upon which relative abundance in the various depth strata was based is too crude to allow reasonable estimates of its variability. Estimates based on alternate models of depth distribution indicate that abundance estimation is relatively sensitive to the choice of models. Additional field work may help refine this model and allow estimation of variance for the parameters I_k in Equation (4).

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HARBOR PORPOISE, *PHOCOENA PHOCOENA*, ABUNDANCE ESTIMATION FOR CALIFORNIA, OREGON, AND WASHINGTON: II. AERIAL SURVEYS

JAY BARLOW,[1] CHARLES W. OLIVER,[1] TERRY D. JACKSON,[2] AND BARBARA L. TAYLOR[3]

ABSTRACT

We conducted aerial surveys in September 1984 and September and October 1985 to determine the abundance of harbor porpoise along the coasts of California, Oregon, and Washington. Two observers and a recorder searched along predetermined transect lines at 0.61 and 1.85 km offshore. Strip transect methods were used. A total of 366 groups of harbor porpoise were seen in the 9,500 linear kilometers that were surveyed. Apparent density was significantly affected by sea state and cloud cover. Using observations made during optimal conditions (clear skies and calm seas), apparent harbor porpoise density averaged 0.56 animals km^{-2}. Behavioral observations from shore and from a helicopter indicated that porpoise are near the surface only 23.9% of the time. To account for this, porpoise density was multiplied by a factor of 3.2, resulting in an adjusted estimate of 1.79 animals km^{-2}. Only a small percentage of the total area inhabited was surveyed under optimal sighting conditions, hence density estimates were not extrapolated to estimate total porpoise abundance. Harbor porpoise density showed similar patterns to those measured from ship surveys, and adjusted aerial estimates are approximately equal to ship estimates.

Harbor porpoise, *Phocoena phocoena*, are subject to mortality in the halibut set net fishery in central California (NMFS[4]; Diamond and Hanan[5]). To evaluate the significance of this mortality, an estimate of population size is needed. Two aerial surveys and three ship surveys were conducted from 1984 to 1986 to gather information on harbor porpoise abundance along the coasts of California, Oregon, and Washington. Observations were also made from shore-based stations and from a helicopter to provide ancillary information needed for population estimation. Results and population estimates from the ship surveys are reported by Barlow (1988). Preliminary results from the 1984 and 1985 aerial surveys were presented by Oliver and Jackson[6] and Oliver[7], respectively. Here we present population density estimates based on the aerial surveys and on shore and helicopter observations.

The aerial surveys were flown in September of 1984 and in September and October of 1985 from Point Conception, CA to Cape Flattery, WA. Surveys were coordinated by the National Marine Fisheries Service (NMFS) in collaboration with the California Department of Fish and Game, the Oregon Department of Fish and Wildlife, and the Washington Department of Wildlife. Survey design was based on information given by Dohl et al.[8] regarding harbor porpoise distribution in California. They reported that harbor porpoise were usually

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[2]National Marine Fisheries Service, Southwest Region, 300 South Ferry Street, Terminal Island, CA 90731; present address: Pacific Marine Center, NOAA, 1801 Fairview Avenue East, Seattle, WA 98102.

[3]National Marine Fisheries Service, National Marine Mammal Laboratory, 7600 Sand Point Way, N.E., Seattle, WA 98115; present address: University of California, San Diego, Department of Biology, La Jolla, CA 92093.

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found within 0.25 nautical miles (nmi) of the shoreline. We therefore designed our aerial surveys to cover a very narrow coastal band. Subsequent information from ship surveys (Barlow 1988) has shown their distribution to extend considerably farther from the coast. Therefore, estimates of porpoise density from aerial surveys apply to a relatively small portion of harbor porpoise habitat. For this reason we do not estimate population size by extrapolating aerial density estimates to the entire area inhabited. The density estimates presented here are used to corroborate estimates based on ship surveys and to estimate density for areas that were too shallow to be surveyed by ship.

Based on previous studies of dive times (Watson and Gaskin 1983; Taylor and Dawson 1984) we expected a proportion of the harbor porpoise to be diving and therefore missed by aerial observers. Shore-based studies were conducted in September 1985 from cliffs in northern Oregon to determine average dive times for west-coast harbor porpoise. Helicopter observations were made in April and May 1986 in Monterey Bay and near Bodega Head, CA to gather dive time information and obtain a direct measure of the fraction of time that harbor porpoise groups are visible from the air. These two samples did not differ significantly from previous samples of harbor porpoise in Alaska, so all samples were pooled to adjust estimates of porpoise density from aerial surveys to account for the probability of missing submerged animals.

METHODS

Aerial Survey Methods

Strip transect methodology (Seber 1973) was used during the aerial surveys. This method assumes that all individuals within a transect strip are detected. Transect lines were flown parallel to the coast line at distances of 0.61 and 1.85 km (0.33 and 1.0 nmi) offshore. Transect strips of equal width were surveyed on both sides of the aircraft. The margins of the strips were denoted by tape marks or streamers on the wing struts. Strips were divided into inside and outside swaths of unequal width (Fig. 1) by a third tape mark or streamer between the other two. When porpoise were sighted within the transect strip, the pilot was directed to leave the transect line and circle over the porpoise to obtain an accurate count of the number within the original group that was sighted. If additional groups or individuals were sighted during this circling, they were excluded from density estimates. Porpoise density, x, was calculated as the number of individuals sighted within a transect, n, divided by the product of the transect width, w, times the distance, d, that was flown:

$$x = n/(W \cdot d) \quad (1)$$

We used both single and twin-propeller, high-wing, 4-passenger aircraft in our surveys. The search team consisted of two observers seated in the right and left passenger seats. A data recorder sat in the copilot's seat and did not search. If the recorder sighted animals that were missed by the observers, these were noted but were not included in density estimates. The planes were flown at an altitude of 213 m (700 feet) and at an airspeed of 158–167 km/h (85–90 knots). The original survey plan called for all sections of the coast to be covered twice on each survey. This was accomplished in 1984, but poor weather in 1985 resulted in the Washington coast and part of the Oregon coast being covered only once. The dates flown and areas covered are given in Table 1.

TABLE 1.—Dates, areas covered, and observer teams during aerial surveys for harbor porpoise. Geographic regions refer to those shown in Figure 2. Observer team refers to a pair of individuals.

Date	Regions covered	Observer team	Distance to shore (km)
9/09/84	7,8	A	0.61
9/10/84	5,7	A	0.61
9/11/84	5,6	A	0.61
9/13/84	1,2,3,4,5	B	0.61
9/14/84	1,2,3,4,5	B	0.61
9/17/84	1,2,3,4	B	0.61
9/18/84	1,2,3,4	B	0.61
9/11/85	6,7	C	0.61
9/16/85	1,2,3	D	0.61
9/17/85	4	D	0.61
9/18/85	4,5	D	0.61,1.85
9/19/85	4,5	D	0.61,1.85
9/20/85	2,3	D	1.85
10/04/85	7,8	E	0.61
10/14/85	1,2,3	D	1.85
10/15/85	4,5	D	1.85

Data gathered on both the 1984 and 1985 surveys were similar in format. Recorded data on sighting conditions included Beaufort sea state, a measure of cloud cover, a code indicating the presence of haze or fog, sun position relative to the aircraft, and a subjective measure of the observers' ability to see into the water through turbidity, surface reflection and diffraction. The latter was called surface penetration and was recorded separately for each of the

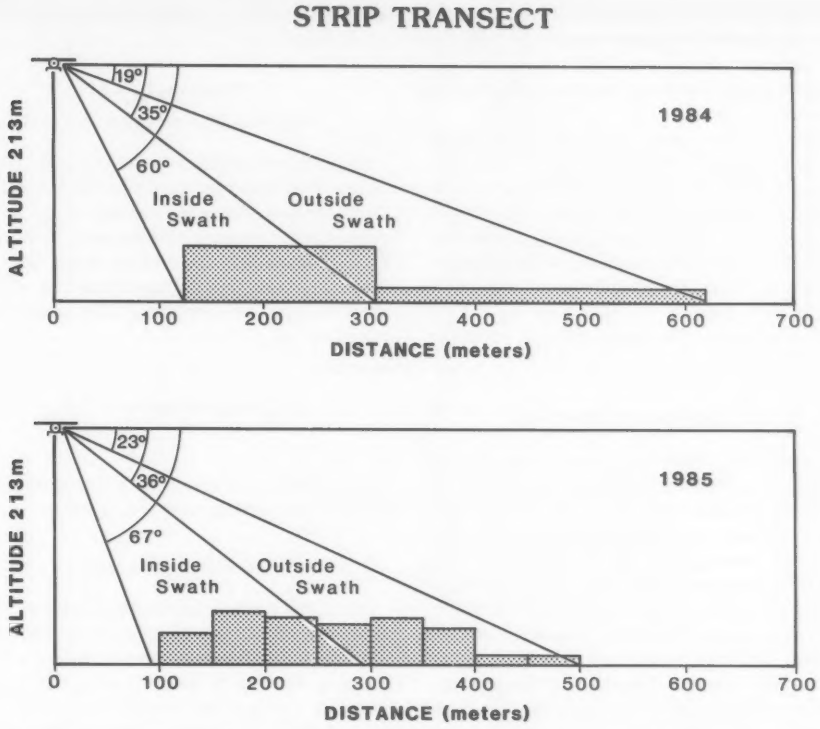

FIGURE 1.—Configuration of transect strip widths and distributions of perpendicular sighting distances for aerial surveys in 1984 and 1985. Angles are given as declinations from horizontal. Histograms indicate the relative number of porpoise seen in the given distance interval.

four swaths (inside and outside on both sides of the aircraft). In severe sun glare conditions, searching was discontinued for one or both swaths on one side of the aircraft. Additional data included individual observer numbers, date, time, and position (measured to 10ths of minutes of latitude and longitude). All of these data were recorded at the beginning and end of continuous transects and whenever conditions changed or a sighting was made. Additional data were recorded for marine mammal sightings, including a code for the species of animal seen, an estimate of the number of individuals, a code indicating on which side of the aircraft the animals were seen, and a code indicating in which of the swaths the animals were found (inside, outside, or, if the animals were not within the designated strips, neither).

An attempt was made to gather the above information in a similar manner for both surveys. Some differences in subjective measures of sighting conditions could, however, be expected because there was no overlap in observers between years. In addition, there were some differences in design between the 1984 and 1985 surveys. In 1984, the inside and outside swaths were from 123 to 305 m and from 305 to 620 m, respectively (as measured from the midline of the transect). The margins of these swaths corresponded to declinations angles of 19°, 35°, and 60° (Fig. 1). In 1985, the swaths were 91–294 m and 294–503 m and corresponded to declination angles of 23°, 36°, and 67° (Fig. 1). In 1984, effort was concentrated on the inside swath and the outside swath was not intended for abundance estimation. The change in swath size was intended to reduce the total area being searched, thus potentially allowing the outer swath to be used for density estimation. In 1985, effort was divided equally between the two swaths. During the 1985

surveys the declination angle to marine mammals was measured when the animals were perpendicular to the aircraft using hand-held inclinometers. Declination angles were not measured during the 1984 survey.

Distance to the coast was monitored using declination angles (19° for 0.61 km and 6° for 1.85 km). On the 1984 survey, this distance was 0.61 km for the entire survey. During the 1985 survey, we surveyed at both 0.61 and 1.85 km from the coast. In 1984, the coast was taken to be the outer limit of the surf zone. In 1985, the coast was taken to be the outer limit of the surf zone or, if kelp beds were present, the outer margin of those beds.

Shore Observation Methods

Observations of harbor porpoise diving behavior were made from rocky headlands in northern Oregon (Tillamook Head, Neahkahnie Mountain, Cape Meares, and Cape Lookout) immediately before the second aerial survey (7–11 September 1985). Observers were equipped with 7×50 binoculars with compasses and ocular reticles and a single 20×120 binocular. Ventilation data were collected whenever possible and included the number of animals at the surface and the length of time spent at the surface. Observations were recited aloud by the observer and were written down by a second person or were recorded onto magnetic tape. The ventilation cycle typically consisted of a period with several surfacing rolls and breaths (which we call a surfacing series) followed by a much longer period of submergence (which we call a dive). This dive cycle corresponds to ventilation pattern B as described by Watson and Gaskin (1983) for harbor porpoise in the Bay of Fundy and the pattern described by Taylor and Dawson (1984) for porpoise in Glacier Bay.

Helicopter Observation Methods

Behavioral observations were also made by three observers in a 4-passenger, jet-turbine helicopter. Upon locating a group of harbor porpoise, a fluorescein dye marker was dropped and the helicopter hovered or circled slowly above the group at an altitude of approximately 300 m. The number of animals, the time they were visible at the surface, and the dive times were recorded, along with information on cloud cover, sea state, and water turbidity. Each behavioral session was given a subjective rating based on how well the observers could follow the group and obtain accurate dive times. Only sessions with good or excellent ratings were included in analyses.

Probability of Missing Submerged Animals

Given that a porpoise would be within the visual range of an observer, the probability that it will be at the surface during the passage of the aircraft is related to the average time it spends at the surface, s, the average time spent below the surface, d, and the window of time during which it is within the visual range of an observer, t. This probability was calculated as

$$Pr(\text{being visible}) = \frac{s + t}{s + d}. \quad (2)$$

The probability of missing a submerged animal is equal to the complement of this value.

Density Estimation

Density of harbor porpoise was estimated as the number of animals seen divided by the area searched (Equation (1)). This raw density estimate was adjusted by dividing by the probability that an animal would be visible from the air at any given instant (Equation (2)). The area searched was estimated as the swath widths times the lengths of the transects. Transect lengths were calculated as the sum of the great circle distances between successive position fixes. Densities were calculated for each of the eight statistical regions used by Barlow (1988) (Fig. 2).

The statistical difference in harbor porpoise density between different sighting conditions or different areas was tested using the raw density estimates. Density estimates for short transects were frequently zero, thus violating the parametric assumptions of normally distributed, homoscedastic error. Nonparametric tests were therefore chosen for density comparisons. In discussing statistical tests, a transect segment refers to the length of transect line between two successive position fixes and are typically <20 km. The measured variables relating to sighting conditions are constant within a segment, and because each sighting is accompanied by a new position fix, a segment will contain at most, one sighting.

Whenever applicable, the Wilcoxon paired-sample test (Wilcoxon 1945) was used to test one factor while controlling for as many other factors as possible. Ten paired measures of density were created

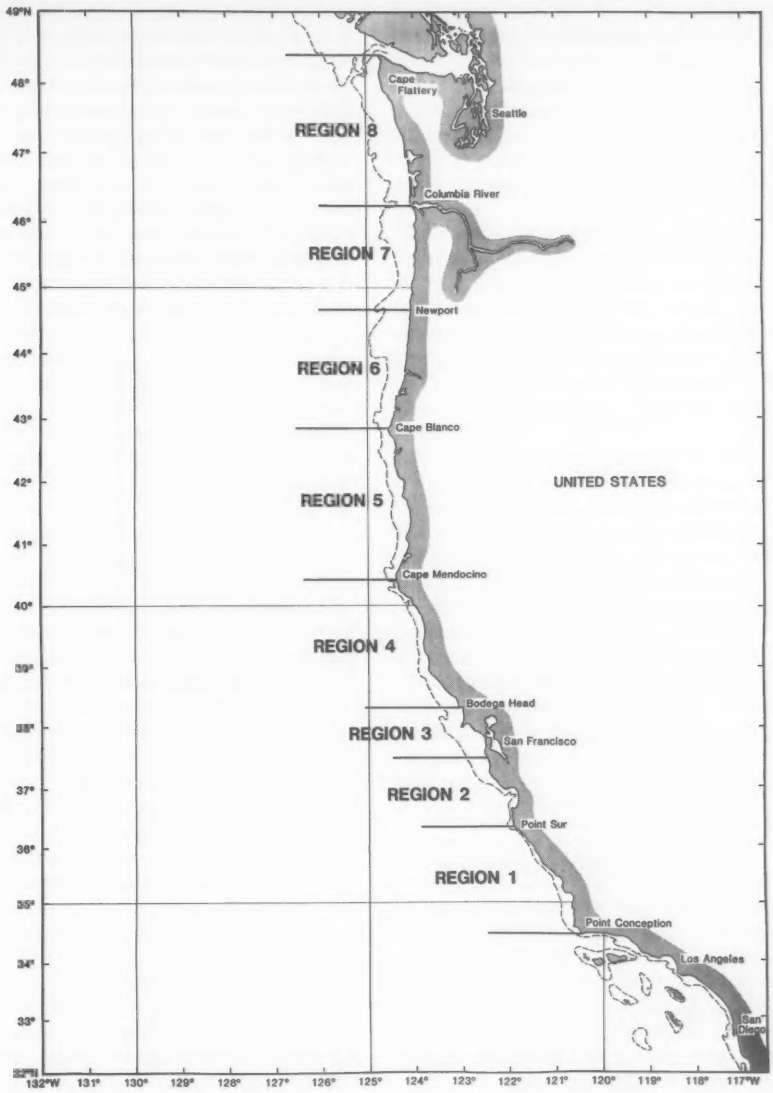

FIGURE 2.—Geographic regions used as strata in density estimation.

by adding all appropriate transect segments to a linear array and dividing that array into 10 equal parts.

When paired tests were not applicable, nonparametric ANOVA models were used. For simple comparisons, the Kruskal-Wallis single-factor analysis of variance was used (Kruskal and Wallis 1952). For two-way comparisons, we used a two-factor extension of the Kruskal-Wallis test (Scheirer et al. 1976). For both tests, three replicate measures of density were created for each cell by randomly assigning transect segments as replicate 1, 2, or 3.

A principal assumption of strip transect methods is that all individuals within the designated strip are counted. Assuming that the fraction of diving animals does not vary with sighting conditions, any effect of sighting conditions on apparent density is likely due to missed animals. In any instance where we show that poorer sighting conditions result in a significant decrease in apparent density (one-tailed for paired tests, two-tailed for ANOVA tests), we eliminate the category of sighting conditions which resulted in that lower estimate. If it is not possible to predict which category would be worse a priori in paired tests (e.g., right swath vs. left), two-tailed probabilities are used. Although we cannot be sure of eliminating all biases using these methods, this pattern of data paring should avoid much of the bias due to missed animals.

RESULTS

In 1984, 247 groups of harbor porpoise (680 individuals) were seen within transect strips which covered a linear distance of 5,763 km. In 1985, we saw 119 groups (384 individuals) in surveys of 3,715 km. Mean group sizes were 2.75 and 3.23 individuals, respectively, for 1984 and 1985. For 1984, the relative frequencies of individuals seen within the inside and outside swaths are illustrated in Figure 1. For 1985, the perpendicular distances from the trackline to the animals were calculated from declination angles, and the relative distribution of sightings is shown in Figure 1 as a function of perpendicular distance.

Inside vs. Outside Swath

For 1984 data, only the inside swaths were used, but for 1985 both inside and outside swaths were considered for density estimation. For 1985, we tested whether the density in the inside swaths was greater than the density of the outside swaths. We only considered cases when the water surface penetration codes were equal in both the inside and outside swaths. Data for inside and outside were thus paired, with all other sighting factors equal. For 1985, the density in the inside was greater (0.09 vs. 0.06 porpoise/km^2), but this difference was not significant ($P > 0.10$).

Surface Penetration

Observers used a subjective coding system to describe their ability to see through the sea surface. Cloud cover, haze, and water turbidity contributed to poor surface penetration. In 1984, observers used codes to indicate good and poor conditions; in 1985, observers used codes for excellent, good, and poor. There were frequent cases when observers recorded different codes for the inside swaths on opposite sides of the plane; hence, paired tests were again appropriate. For 1984, we tested whether density in the "good" category was higher than density in the "poor" category. When surface penetration was different in the inside swaths on opposite sides of the plane, mean density in the "good" category was higher than in the "poor" category (0.16 vs. 0.12 porpoise/km^2), but this difference was not significant ($P > 0.25$). For 1985, no tests were necessary because the mean density in "excellent" category was lower than in the "good" category, and likewise, density in the "good" was lower than in the "poor" category. All categories of water surface penetration were included in subsequent analyses.

Effects Due to Observers and Side of the Plane

Sightings were classified based on which observer made the sighting and on whether the sighting was on the inshore or offshore side of the aircraft. In fact, these two classifications were confounded in 1985 because the two principal observers were situated on the same sides of the aircraft for most of this survey. Effects of these classifications on density estimation were considered together. Survey teams were defined as pairs of observers who worked together. There were two such teams for 1984 and three for 1985 (Table 1). Only one of the teams in 1985 had sufficient numbers of sightings to be considered here. Statistical tests were based on paired cases during which both members of the sighting team were searching.

For 1984, porpoise density on the offshore side of the airplanes was greater than on the inshore side for both team A and team B (Table 2). The difference in density estimates between observers was less than the difference between inshore and off-

TABLE 2.—Relative harbor porpoise densities (km^{-2}) for teams of observers. Density estimates are stratified by inshore and offshore sides of the aircraft and by individual observers.

Observer team	Inshore	Offshore	Observer 1	Observer 2
A	0.275	0.425	0.320	0.380
B	0.168	0.244	0.232	0.179
D	0.281	0.164	0.300	0.146

shore (Table 2), and neither was statistically significant. For 1985, the opposite was seen; the density on the inshore side was greater than on the offshore side and this difference was less than the difference between observers (Table 2), but again, neither difference was statistically significant. In 1984, both observers had previous experience doing aerial surveys, but in 1985, the observer with the lower density estimates had no previous experience in cetacean surveys. Experience may be a factor in density estimates from strip transects, but since the inexperienced observer was always on the same side of the plane, it was not possible to test this with a factorial design.

Area and Sea State

Analysis of research vessel data (Barlow 1988) indicated two geographic regions in California with low porpoise density (regions 1 and 3 in Figure 2). We tested whether density observed from aircraft are also lower in these areas. Because observation conditions may have differed in the two areas, we included sea state as a second factor in a two-way ANOVA. Mean values are presented in Table 3. For 1984, three categories of sea state were used: Beaufort 0 & 1, Beaufort 2, and Beaufort 3 and greater. The effect due to area was significant ($P < 0.001$), with the area that showed low density in the ship surveys also showing lower density in the aerial survey. For 1985, only the first two categories of sea state were used due to insufficient data at Beaufort 3 and greater. Again the effect of area was significant ($P < 0.025$), and the same trends were seen. In neither case were the effects of sea state or the interaction effects significant. To eliminate area effects from confounding statistical results, only data for the larger, high-density area were included in subsequent tests. The low-density area was included in later estimates of overall harbor porpoise density.

TABLE 3.—Uncorrected harbor porpoise densities (km^{-2}) for the two-way comparison of area and sea state. Low-density areas refer to two regions in California that were found to have much lower than average density in previous ship surveys (see text). High-density areas include all other regions. Only inside swaths were included. Numbers in parentheses refer to area (km^2) surveyed under the given condition. Densities in brackets were excluded from two-way comparisons due to the small area covered in one cell.

Beaufort sea state	1984 survey		1985 survey	
	Low-density area	High-density area	Low-density area	High-density area
0 & 1	0.027 (183)	0.579 (264)	0.089 (124)	0.762 (126)
2	0.081 (308)	0.312 (1012)	0.089 (214)	0.183 (425)
3+	0.102 (79)	0.191 (252)	[0.000] (28)	[0.049] (566)

Sea State and Cloud Cover

Both sea state and cloud cover can affect sighting conditions. Because both are affected by local weather, the effects of these are likely to be confounded. These two factors were therefore tested simultaneously in a two-way ANOVA. We considered only the inside swath and excluded the two low-density regions. We used the same sea state categories as above. The sky was categorized as clear if cloud cover was <25% and cloudy if >25%. Mean porpoise densities for each category are given in Table 4. It was necessary to exclude the Beaufort 0 & 1 category for 1985 because only 52 km were surveyed in cloudy conditions for these sea states. The effect due to cloud cover was significant for 1984 ($P < 0.025$) and 1985 ($P < 0.05$). The effect of sea state and the interaction effect of sea state and cloud cover were not significant for either survey ($P > 0.10$). Transect segments with >25% cloud cover were excluded from subsequent analyses.

TABLE 4.—Uncorrected harbor porpoise densities (km^{-2}) for the two-way comparison of sea state and cloud cover. Clear refers to <25% cloud cover, and cloudy refers to >25%. Data include only inside swaths in high-density areas. Numbers in parentheses refer to area (km^2) surveyed under the given condition. Densities in brackets were excluded from two-way comparisons due to the small area covered in one cell.

Beaufort sea state	1984 survey		1985 survey	
	Clear	Cloudy	Clear	Cloudy
0 & 1	1.340 (81)	0.240 (183)	[0.832] (115)	[0.000] (11)
2	0.371 (572)	0.236 (440)	0.271 (232)	0.078 (193)
3+	0.266 (162)	0.056 (90)	0.088 (272)	0.014 (294)

Sea State

The effect of sea state was tested alone using only the transect segments which occurred under clear skies (<25% cloud cover) and within the high-density areas. For 1984, only the inside swath was included.

For 1985, both inside and outside swaths were included. As in previous stratifications, apparent density clearly decreased with increasing sea state (Table 5). This effect was significant for surveys in both 1984 ($P < 0.05$) and 1985 ($P < 0.005$). Transect segments surveyed during sea states of 2 or greater were excluded in subsequent analyses.

TABLE 5.—Uncorrected harbor porpoise densities (km^{-2}) for the stratification based on sea state. Data include only high-density areas surveyed when cloud cover was <25%. Data for 1984 include inside swaths only; data for 1985 include inside and outside swaths. Numbers in parentheses refer to area (km^2) surveyed under the given condition.

Beaufort sea state	1984 survey	1985 survey
0 & 1	1.340 (81)	0.807 (234)
2	0.371 (572)	0.193 (471)
3+	0.266 (162)	0.058 (553)

Between Survey Differences

We considered the 1984 survey and the 1985 surveys at 0.61 km and 1.85 km from shore as three independent estimates of harbor porpoise density. Because apparent density was shown to vary greatly with sighting conditions and because sighting conditions varied between surveys, it was necessary to compare these three under similar conditions.

The highest (and presumably least biased) densities were obtained when sea state was Beaufort 0 & 1 and when cloud cover was <25%. Between survey comparisons under these conditions are given in Table 6 for the eight geographic regions given in Figure 2. For 1985, there were no transect segments at 0.61 km from shore under the conditions Beaufort 0 & 1 and clear skies. For 1984, only three regions contained more than 10 km^2 of searching effort at 0.61 km from shore. For 1985, only four areas had any searching effort at 1.85 km from shore. The only direct density comparisons with reasonable sample sizes are for region 1 (0.000 vs. 0.048 porpoise/km^2) and region 3 (0.111 vs. 0.110 porpoise/km^2) (respectively for 1984 and 1985). The densities for all regions pooled (0.671 and 0.510 porpoise/km^2) are similar, but because of the small sample size and geographic variation in sampling, a statistical test of this difference is meaningless.

In comparing surveys, sample size and regional coverage improved slightly when Beaufort 2 was considered (still allowing a maximum of 25% cloud cover) (Table 7). For 1984, coverage was relatively complete in all regions. For 1985, coverage at 0.61 km from shore was limited to regions 2–4, and coverage at 1.85 km was limited to regions 1–5. Comparing the two surveys in 1985, distance from shore made little difference in overall density for all regions combined, and neither survey had consistently higher values than the other. Comparing the 1984 survey to the two 1985 surveys, the former had a higher overall density for all regions combined, but again this difference was not consistent among regions. Sample size and regional coverage were again too poor for meaningful statistical tests.

TABLE 6.—Uncorrected harbor porpoise densities (km^{-2}) in eight geographic regions surveyed during Beaufort 0 & 1 conditions. Data for 1984 are based on inside swaths of transects flown 0.61 km from the coast. Data for 1985 are based on inside and outside swaths of transects flown at 0.61 and 1.85 km from the coast. Only those segments surveyed when cloud cover was <25% are included. Numbers in parentheses refer to area (km^2) surveyed under the given condition.

Geographic region	1984 survey density 0.61 km	1985 survey density 0.61 km	1985 survey density 1.85 km
1	0.000 (43)	— (0)	0.048 (103)
2	0.000 (1)	— (0)	0.609 (51)
3	0.111 (45)	— (0)	0.110 (55)
4	0.953 (6)	— (0)	0.862 (183)
5	1.120 (9)	— (0)	— (0)
6	1.374 (64)	— (0)	— (0)
7	5.745 (1)	— (0)	— (0)
8	— (0)	— (0)	— (0)
All regions	0.671 (170)	— (0)	0.510 (392)

Ventilation Patterns

Harbor porpoise did not appear to react to the helicopter during aerial observations; they were visible throughout a surfacing series and were not visible during dives. Knowing this, we were able to use data on surfacing series and dive times to determine the fraction of time harbor porpoise would be visible from the air. Data on ventilation patterns

were available from the helicopter study in California (13 groups were observed, mean group size was 2.7), the Oregon shore observations (11 groups, mean group size was 4.2), and a previous shore study in Glacier Bay, AK (28 solitary individuals). The mean times spent in surfacing series were 34.2, 24.6, and 30.0 seconds (respectively for the three studies). The corresponding mean dive times did not differ significantly between study sites ($P > 0.05$ using pairwise t-tests). Using the pooled data set ($n = 52$), the mean time spent in a surfacing series was 30.02 seconds (SE = 1.95) and the mean time spent in a dive was 95.81 seconds (SE = 5.32). The percentage of time spent at the surface is 23.9%.

Average and Adjusted Density Estimates

Harbor porpoise densities under optimal conditions (Beaufort 0 & 1 and <25% cloud cover) were averaged for the two surveys, weighting by transect length (Table 8). Given an average survey speed of 160 km/h and assuming that the window for harbor porpoise observation is 400 m long, the time window during which a point would be visible is 9.0 seconds. Using this estimate and the surface and dive times estimated above, the probability that a porpoise will be seen is estimated as 0.310 from Equation (2). An instantaneous count would therefore underestimate porpoise abundance by a factor of 3.2. Average values were therefore multiplied by this factor (Table 8).

TABLE 7.—Uncorrected harbor porpoise densities (km^{-2}) in eight geographic regions surveyed during Beaufort 2 conditions. Data for 1984 are based on inside swaths of transects flown 0.61 km from the coast. Data for 1985 are based on inside and outside swaths of transects flown at 0.61 and 1.85 km from the coast. Only those segments surveyed when cloud cover was <25% are included. Numbers in parentheses refer to area (km^2) surveyed under the given condition.

Geographic region	1984 survey density 0.61 km	1985 survey density 0.61 km	1985 survey density 1.85 km
1	0.000 (107)	— (0)	0.184 (103)
2	0.092 (109)	0.102 (59)	0.103 (68)
3	0.196 (117)	0.062 (48)	0.287 (52)
4	0.562 (180)	0.282 (110)	0.070 (57)
5	0.489 (119)	0.459 (6)	0.234 (171)
6	0.439 (57)	— (0)	— (0)
7	0.114 (70)	— (0)	— (0)
8	0.268 (37)	— (0)	— (0)
All regions	0.295 (796)	0.192 (224)	0.188 (452)

DISCUSSION

Results indicate that sighting conditions must be very good in order to estimate harbor porpoise abundance from aerial strip transects. Both sea state and cloud cover had very large and significant effects on apparent density. Limiting observations to the best categories of sea state (Beaufort 0 & 1) and cloud cover (<25%) can be used to minimize the bias due to missed animals. These conditions are, however, rare and only occurred during 5.3% and 10.3% of the transects in 1984 and 1985. The actual occurrence of these conditions is even more rare if one considers flights that were cancelled due to bad weather.

The effects on sea state and cloud cover on sighting conditions were predicted by observers before analysis of survey data was begun. Most harbor porpoise were first seen when submerged a small distance below the surface. Surfacings were relatively inconspicuous to aerial observers and were not an important cue in sighting porpoise. Both sea state and cloud cover affect the ability of observers to see through the water's surface and to spot submerged animals. Increasing sea state causes more refraction of light at the water's surface, increases glit-

TABLE 8.—Harbor porpoise densities (km^{-2}) in eight geographic regions from a) a weighted average of uncorrected estimates from 1984 and 1985 aerial surveys, b) the same average adjusted by a factor of 3.2 to account for submerged porpoise that were missed by aerial observers, and c) a weighted average for the 1984 and 1985 ship surveys. Aerial estimates are based on observations made under conditions of Beaufort 0 & 1 and with <25% cloud cover. Ship estimates include Beaufort sea states of 0, 1, and 2.

Geographic region	Area surveyed (km^2)	Aerial estimates		Research vessel estimates
		Uncorrected a	Corrected b	c
1	146	0.03	0.10	0.05
2	1	—	—	0.66
3	100	0.11	0.35	0.04
4	189	0.86	2.75	3.68
5	9	1.12	3.58	1.18
6	64	1.37	4.38	2.88
7	1	—	—	3.43
8	0	—	—	1.42
All regions	562	0.559	1.79	1.73

tery reflection of sunlight, and causes whitecaps which obscure subsurface observation. Cloud cover decreases penetration of sunlight into the sea and causes its surface to appear dark and glazed. It is therefore not surprising that calm seas and clear skies result in higher apparent densities.

It is more surprising that apparent density did not vary with observer's subjective appraisal of surface penetration. This may have been because surface penetration was only tested in paired cases for which sea state and cloud cover were identical. In these cases, differences in surface penetration may have been due primarily to subjective differences in the way individual observers were coding it. If all cases are considered, surface penetration is very highly correlated with sea state and cloud cover and probably could be used as an alternative measure of sighting conditions. We prefer, however, to use sea state and cloud cover because their measure is less subjective than surface penetration and could more easily be used by other researchers.

Missed Animals

A principal assumption of strip transect methods is that all individuals within the strip are counted. We cannot necessarily meet this assumption just by eliminating the categories of sighting conditions with significantly lower density. In fact, it is possible that this method of selectively eliminating data could overestimate density by eliminating a category of sighting conditions which (by random chance) had a significantly lower density. We do not believe that this is likely in the cases of sea state or cloud cover because the trends were the same for both surveys and because the categories that were eliminated were judged a priori as being poorer sighting conditions. We believe that porpoise density is more likely underestimated due to missed animals. Kraus et al. (1983) found that observers in aircraft saw only 14% of the harbor porpoise groups known to be present based on shore-based observations. Missed animals may include some individuals that were near the surface and visible but were not seen, as well as others that were diving and were too deep to be seen.

We infer that some near-surface animals were missed based on three reasons. First, apparent density decreased with increasing sea state and cloud cover, hence near-surface animals must be missed in (at least) the poorer conditions. (An alternative explanation is that porpoise spend less time near the surface when sighting conditions are poor.) Second, of the two principal observers in 1985, the less experienced observer may have missed more porpoise. Third, in five instances in 1984 and one instance in 1985, the data recorder saw harbor porpoise in the inside swath that were missed by the observer. In three of these cases, conditions were Beaufort 1 with <25% cloud cover. Recorders searched only occasionally as conditions permitted, so it is not possible to use these data to quantify how many near-surface animals were missed under good conditions.

Based on behavioral observations, we can also be certain that some harbor porpoise are missed because they are too deep to be seen. Water visibility was typically only 2–5 m during the surveys. Aerial observers have seen harbor porpoise dive out of view during the passing of the plane or while circling. Harbor porpoise were not visible from the helicopter during dives, even in very calm water. Some fraction of porpoise must be missed because they are too deep to be seen.

We have tried to account for the fraction of diving animals by dividing density estimates by the fraction of time harbor porpoise are known to be near the surface (i.e., within surfacing series). Uncorrected estimates of harbor porpoise density are based on the assumption that porpoise are never too deep to be seen; this undoubtedly results in an underestimate of porpoise density. Our method of adjusted estimates of porpoise density assumes that, when diving, porpoise are always too deep to be seen; this has been corroborated by helicopter observations. The latter estimate should therefore be closer to the true value of porpoise density (if biases due to other factors have been eliminated).

Offshore Distribution of Harbor Porpoise

In 1985, aerial transects were flown at 0.61 and 1.85 km from the shore. The latter value was chosen to correspond approximately to the ship transects along the 10-fathom (18.3 m) isobath. The intent was to directly compare aerial estimates of density to estimates made from ships at the same distance from shore (considered below) and to provide a means to extrapolate ship estimates to regions that were too shallow to survey by ship. In regard to the latter, we wish to know whether harbor porpoise density at 0.61 km from shore is different from that at 1.85 km.

In 1985, surveys at 0.61 km were never flown under good sighting conditions (Beaufort 0 & 1 and <25% cloud cover), so direct comparisons between 0.61 and 1.85 km are not possible. Considering only the best category of sighting conditions, it is possi-

ble to compare 1985 transects at 1.85 km with 1984 transects at 0.61 km in geographic regions 1 and 3 (Table 6). Sample sizes are very small, but densities are roughly comparable (0.070 vs. 0.057, respectively for 1.85 and 0.61 km from shore). Sample sizes in 1985 can be increased if Beaufort 2 is considered instead of Beaufort 0 & 1 (still with <25% cloud cover). Based on geographic regions 1 through 5, porpoise densities are virtually identical at 1.85 and 0.61 km from shore (0.188 vs. 0.192, respectively, Table 7).

In a preliminary model of harbor porpoise depth distribution, Barlow (1988) hypothesized that harbor porpoise density is constant from the shore to the 75 m isobath. Ship data did not, however, include any transects inshore of 18.3 m depth. In this shallow area, the model was not based on any data. Although sparse, data from aerial surveys show that densities are similar in areas that were surveyed by ship (1.85 km from shore) and in areas that were too shallow to be surveyed by ship (0.61 km from shore). These data are consistent with the model proposed by Barlow.

Comparison of Ship and Aerial Density Estimates

Estimates of harbor porpoise density from 1984 to 1985 ship surveys (Barlow 1988) can be compared with adjusted and unadjusted estimates from the aerial surveys (Table 8). The overall density for all regions is higher for the ship surveys than for the unadjusted aerial. Adjusted estimates from the aerial surveys are very close to the overall estimates from ship surveys.

Previous comparisons have been made of sighting efficiency from aerial and surface vessel platforms (Kraus et al. 1983). They found that observers on boats saw 52% of the harbor porpoise groups seen by shore-based observers, whereas aerial observers saw only 14%. Based on this, density from aerial surveys might be expected to be only 27% of that from ship surveys. In the present study, unadjusted density based on aerial surveys is 32% of the density from ship surveys. The two studies are not directly comparable, however. Weather conditions are not reported by Kraus et al. (1983) and may have included less than optimal sighting conditions. It should be noted that the fraction of harbor porpoise groups seen by aerial observers in their study (14%) is even lower than the fraction of harbor porpoise we assumed would be in surfacing series and hence near the surface (23.9%). It is possible that behavioral differences between harbor porpoise from the two coasts (such as travelling or behavior mode "A" noted by Watson and Gaskin (1983)) could account for some of the differences noted above.

Estimates based on ship surveys cannot, of course, be considered the true density of harbor porpoise. The overall estimate based on ship surveys is relatively imprecise (C.V. = 49%) and may be biased (Barlow 1988). The ship survey estimate is, however, superior to current estimates from aircraft for several reasons. Line transect methods were used on the ship surveys, and the principal assumption of this method (that 100% of the animals in the immediate vicinity of the trackline are seen) is more easily met than the comparable strip transect assumption (that 100% of the animals within a strip are seen). Acceptable sighting conditions for ship surveys included Beaufort 0 & 1, and 2 and were not restricted by cloud cover (Barlow 1988). This allowed more complete geographic coverage than did aerial surveys. Also, the ship travelled much slower than the aircraft (10 knots vs. 80–90 knots), thus the probability of missing a diving individual was much less. Barlow (1988) calculated that diving animals located near the trackline would be missed by observers on ships only if dive times exceeded 2 minutes. Finally, estimates of the correction factor to account for submerged animals is relatively imprecise. Additional observations on ventilation patterns may allow further refinements in density estimates based on aerial surveys.

RECOMMENDATIONS

The design of future surveys for harbor porpoise could be improved based on the results obtained from our aerial surveys. We found that sighting conditions deteriorated rapidly with both increasing cloud cover and rougher sea states. To the extent that is possible, aerial surveys for harbor porpoise should only occur on clear days with little wind. Observations made by the data recorders indicate that some harbor porpoise will be missed even in good sighting conditions. If strip transects are used, experiments with two independent teams of observers searching at the same time could be used to quantify the fraction of animals that are missed by using just one team. Given that fewer harbor porpoise were seen between 400 and 500 m of the track line, we also suggest that, when surveying at 213 m altitude, the strip widths should be decreased to only include the area between 100 and 400 m.

We believe, however, that the problem of missing harbor porpoise could be reduced if line transect methods were used in place of strip transects. Line

transect methods assume that 100% of all animals are seen directly along the trackline and use statistical techniques to estimate the number of animals that are missed as a function of the distance from this trackline. Line transects would require use of an aircraft with unobstructed downward visibility through a belly window and use of a third observer who could view animals directly under the aircraft.

Harbor porpoise are now known to occur further from the shoreline than was believed at the beginning of this study (Barlow 1988). In future surveys, transect lines should be placed so as to cover a greater fraction of the harbor porpoise habitat.

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EVALUATION OF VARIABILITY IN SABLEFISH, *ANOPLOPOMA FIMBRIA*, ABUNDANCE INDICES IN THE GULF OF ALASKA USING THE BOOTSTRAP METHOD

MICHAEL F. SIGLER AND JEFFREY T. FUJIOKA[1]

ABSTRACT

Relative population numbers (RPN's) and length compositions were computed for sablefish, *Anoplopoma fimbria*, in the Gulf of Alaska from the results of the Japan-United States cooperative longline survey from 1979 to 1986. A statistical evaluation of annual changes in the RPN's using the bootstrap method is demonstrated and showed that sablefish abundance increased significantly from 1979 to 1986, an increase likely due to recruitment of two strong year classes. The effect of missing data on the bootstrap calculations was examined and found to be negligible.

Early in this century, United States and Canadian fishermen began harvesting sablefish, *Anoplopoma fimbria*, in nearshore waters from California north to southeastern Alaska, but sablefish were not heavily exploited until Japanese longline vessels began fishing in the Bering Sea in 1958. Japanese catches off both the U.S. and Canadian coasts rose dramatically in the following two decades. After passage of the Fishery Conservation and Management Act, foreign catches were reduced and the domestic allocation was increased. The domestic catch eventually increased nearly fivefold, thereby replacing the foreign fishery, and in 1985, sablefish in the Gulf of Alaska were harvested entirely by domestic fishermen.

Before the reduction of the foreign fishery, information on sablefish abundance consisted of statistics on catch per unit effort from the Japanese longline fishery. In 1978, the Fisheries Agency of Japan and the U.S. National Marine Fisheries Service (NMFS) began a cooperative longline survey along the continental slope of Alaska to assess the abundance of sablefish and Pacific cod, *Gadus macrocephalus*. The survey, conducted annually, has provided eight consecutive years (1979–86) of data for the Gulf of Alaska, seven years (1980–86) of data for the Aleutian region, and five years (1982–86) of data for the eastern Bering Sea. The first year of the survey, 1978, was experimental.

Relative population numbers (RPN's) and length compositions from the longline survey results from 1979 to 1985 have been estimated previously by Sasaki (1986). In this study, the observed increase in the RPN's for sablefish in the Gulf of Alaska is evaluated statistically and an explanation of the probable source of the increase is discussed.

Statistical analysis of the survey results is based on the bootstrap method (Efron 1982; Efron and Gong 1983). This method is a relatively new statistical procedure that has been little used in fisheries analysis. Thus, this paper also demonstrates an application of the bootstrap method to statistical evaluation of fishery survey data.

SURVEY METHODS

The Gulf of Alaska portion of the Japan-U.S. cooperative longline survey, conducted annually each summer from 1979 to 1986, covered five International North Pacific Fisheries Commission (INPFC) statistical areas: Shumagin, Chirikof, Kodiak, Yakutat, and Southeastern (Fig. 1). One of a total of 47 stations each ranging in depth from about 100 to 1,000 m was sampled daily by longline. The longline was 16 km long and consisted of 160 hachis (the Japanese word for "skate" or length of longline); each hachi was 100 m long and consisted of 45 hooks baited with squid. Soak time, the time between setting and retrieval, varied from 3 hours at the beginning of the longline gear to 7 or 8 hours at its end. The depth at which the fish were caught was estimated by measuring the depth of water under the vessel with an echo sounder every fifth hachi. The fish caught were tallied by species and hachi as the longline was brought aboard, then they were weighed and their length was measured. Most

[1]Northwest and Alaska Fisheries Center Auke Bay Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 210155, Auke Bay, AK 99821.

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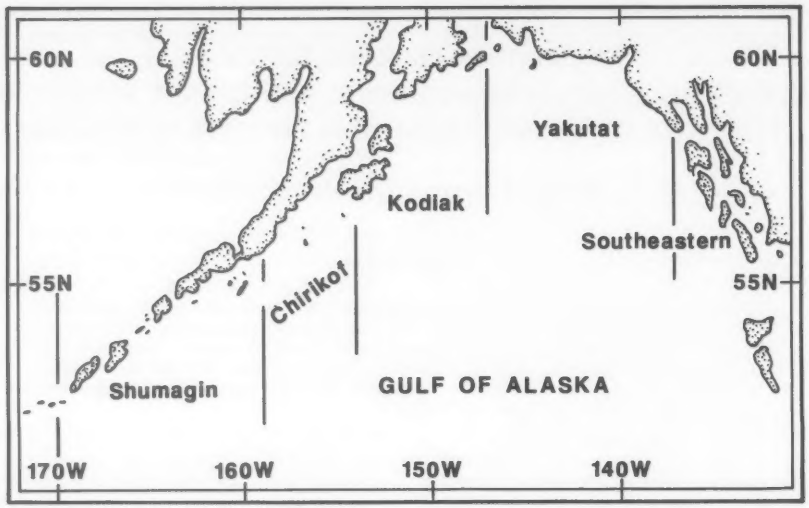

FIGURE 1.—International North Pacific Fisheries Commission statistical areas sampled during the Gulf of Alaska portion of the Japan-U.S. cooperative longline survey, 1979–86.

sablefish were sexed, some were tagged and released, and others were sampled for otoliths and scales. Detailed survey methods are described in Sasaki et al. (1983).

STATISTICAL METHODS

The catch data were stratified because of differences in the catch rate by depth. Assignment of the

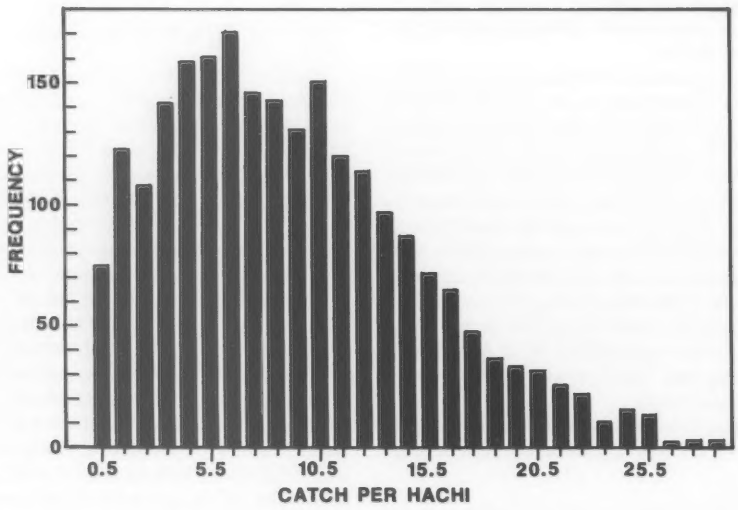

FIGURE 2.—Frequency distribution of sablefish catch per hachi (numbers) by year, station, and strata, 1979–86.

catch data to a stratum was based on the recorded depth of every fifth hachi or the interpolated depth of each of the intervening four hachis. The number of strata totaled nine, with the first stratum representing 101–200 m, the second representing 201–300 m, and so on. A catch per hachi value was calculated for each stratum of a station (Fig. 2), and the resultant values within each statistical area were averaged.

Not all strata were sampled at each station and as a result, sometimes no stations were sampled within certain strata (Table 1). Although not sampled one year, these strata generally were sampled the previous year, because of slight annual differences in the depths sampled at each station. Catch per hachi values $CPUE_{i,j}$ were estimated for stations within the unsampled strata from the catch per hachi values for sampled stations from the previous year and the annual change in the catch per hachi values in the adjacent stratum. For each station:

$$CPUE_{i,j} = CPUE_{i-1,j} * CPUE_{i,j'}/CPUE_{i-1,j'}$$

where i = year, j = stratum, and j' = the adjacent stratum. Catch per hachi values were estimated only for stations within unsampled strata. If one or more stations within a stratum were sampled, then no catch per hachi values were estimated for the unsampled stations. The effect of these missing values on the survey results will be discussed later.

Relative population numbers were calculated from the catch per hachi values to index annual changes in sablefish abundance. As in Sasaki (1985), the average catch per hachi was multiplied by the areal size of each stratum and statistical area to calculate an RPN for each stratum and statistical area. The areal sizes used to calculate the RPN's are for the continental slope only (Table 2), which corresponds to the area covered by the survey. The resultant RPN's were summed across strata to calculate an RPN for each statistical area, and these RPN's were summed

TABLE 1.—Number of stations sampled by year, INPFC area, and depth during the Japan-U.S. cooperative longline survey, 1979–86.

		INPFC statistical area							INPFC statistical area				
Year	Depth (m)	Shumagin	Chirikof	Kodiak	Yakutat	Southeast	Year	Depth (m)	Shumagin	Chirikof	Kodiak	Yakutat	Southeast
1979	101–200	7	4	6	6	2	1983	101–200	9	5	7	8	3
	201–300	7	5	7	10	5		201–300	10	6	9	11	9
	301–400	7	5	8	11	6		301–400	10	5	9	11	8
	401–500	7	5	9	11	6		401–500	10	6	9	11	8
	501–600	6	4	9	11	6		501–600	10	5	9	11	8
	601–700	6	4	8	11	5		601–700	9	5	9	11	7
	701–800	6	4	7	11	5		701–800	8	4	8	11	7
	801–900	5	1	4	9	4		801–900	5	4	4	10	7
	901–1,000	4	1	2	4	1		901–1,000	2	0	1	5	2
1980	101–200	9	5	8	7	4	1984	101–200	10	7	7	8	2
	201–300	10	6	8	10	6		201–300	10	7	9	11	9
	301–400	10	6	8	10	8		301–400	10	6	9	11	8
	401–500	10	6	9	10	8		401–500	10	6	9	11	8
	501–600	10	5	9	10	7		501–600	10	5	9	11	8
	601–700	9	5	9	9	7		601–700	8	5	8	11	8
	701–800	6	4	8	9	7		701–800	7	5	6	10	8
	801–900	6	2	3	7	4		801–900	3	0	3	7	5
	901–1,000	5	1	2	6	1		901–1,000	0	0	0	6	1
1981	101–200	9	6	7	8	1	1985	101–200	9	6	6	7	1
	201–300	10	6	9	11	9		201–300	10	7	8	11	9
	301–400	10	6	9	11	9		301–400	10	6	9	11	8
	401–500	10	6	9	11	9		401–500	10	6	9	11	7
	501–600	10	6	9	11	9		501–600	10	6	9	11	8
	601–700	9	4	9	11	9		601–700	9	5	9	11	8
	701–800	7	2	7	11	9		701–800	7	4	9	10	8
	801–900	6	1	5	7	7		801–900	4	4	4	11	6
	901–1,000	2	0	1	2	1		901–1,000	0	0	0	5	2
1982	101–200	9	5	7	10	4	1986	101–200	9	5	7	7	2
	201–300	9	6	9	11	9		201–300	10	6	9	11	9
	301–400	10	5	9	11	8		301–400	10	6	9	11	8
	401–500	10	6	9	11	8		401–500	10	6	9	11	8
	501–600	10	5	9	11	8		501–600	10	6	9	11	8
	601–700	10	5	9	11	8		601–700	10	4	9	11	8
	701–800	9	4	8	11	7		701–800	10	3	8	11	8
	801–900	7	4	6	9	6		801–900	5	2	7	11	8
	901–1,000	3	3	5	8	3		901–1,000	1	1	3	5	1

TABLE 2.—Slope area sizes (km^2).

Depth (m)	Slope area (km^2)[1]				
	Shumagin	Chirikof	Kodiak	Yakutat	Southeast
201–400	4,001	2,350	3,106	2,988	1,781
401–600	2,269	1,766	2,255	1,666	822
601–800	1,629	1,955	1,923	1,470	1,006
801–1,000	1,248	2,012	2,296	1,489	1,165
201–1,000	9,147	8,083	9,580	7,613	4,774

[1]Shumagin, Chirikof, and Kodiak areas and Yakutat area from long. 147–144°W; data from E. Brown (NWAFC Seattle Laboratory, NMFS, NOAA, 7600 Sand Point Way NE, Seattle, WA 98115, pers. commun. December 1985). Yakutat area from long. 144–137°W. and Southeastern area; data from R. Haight (NWAFC Auke Bay Laboratory, NMFS, NOAA, P.O. Box 210155, Auke Bay, AK 99821, pers. commun. 1986).

across statistical areas to calculate an RPN for the Gulf of Alaska. The bootstrap method (Efron 1982; Efron and Gong 1983) then was applied to the resultant RPN's to test the statistical significance of annual changes in the RPN's.

The bootstrap method is a nonparametric statistical procedure based on Monte Carlo methods (see Shreider [1966] for a description of Monte Carlo methods). The bootstrap method is a new technique not common in the fisheries and ecology literature, but examples of its application to survey design and biomass estimation can be found in Kimura and Balsiger (1985) and Haslett and Wear (1985), respectively. In addition, Rao and Wu (1984) proved the applicability of the bootstrap method to stratified sampling, which is the sampling method used in the longline survey. The bootstrap method is useful when parametric assumptions are difficult to justify; no parametric estimate is readily available for the accuracy of a statistic, e.g., a sample median; or the procedure to compute the statistic of interest is complicated. Simply described, the bootstrap method works as follows: Given the observed data set $<X_1, X_2, \ldots, X_n>$, the sample $<X_1^*, X_2^*, \ldots, X_n^*>$ is drawn by independent random sampling with replacement from the observed data set and the desired statistic (e.g., a median) is computed from the sample. The resultant statistic is termed the bootstrap replicate. In the next step, the sample is drawn and the bootstrap replicate is computed some large number B times. The resultant B bootstrap replicates form the bootstrap distribution. An estimate of the accuracy of the median, a standard error, then can be calculated from the bootstrap distribution by standard methods.

In this study, we used the bootstrap method to test the null hypothesis that the difference $RPN_{i',k} - RPN_{i,k} = 0$, for any $RPN_{i,k}$, where i = year (1979–86), i' = any subsequent year, and k = statistical area (Shumagin, Chirikof, Kodiak, Yakutat, and Southeastern). The bootstrap method was used because parametric assumptions are difficult to justify for the longline survey data and the procedure to compute the statistic of interest, the variance of the RPN, is tedious and error prone. In our application of the bootstrap method, stations were randomly sampled with replacement within each area. A value denoted $RPN_{i,k}^*$ was computed from the catch per hachi values of the sampled stations by the method of RPN calculation described previously. Stations then were sampled with replacement from year i' within each area, a second value denoted $RPN_{i',k}^*$ was computed, and the difference $RPN_{i',k}^* - RPN_{i,k}^*$ was found. Sampling with replacement from the 2 years and the computation of the difference were repeated 1,000 times producing a bootstrap distribution of 1,000 differences.

Efron and Tibshirani (1986) outlined three methods for setting an approximate confidence interval from a bootstrap distribution for a statistic of interest, here the difference $RPN_{i',k} - RPN_{i,k}$. Use of the simplest method, the percentile method, is considered correct if the bootstrap distribution of the statistic of interest is described by a normal distribution (Efron and Tibshirani 1986). The normality of the bootstrap distribution for the difference was tested using the D'Agostino D Test (D'Agostino and Stephens 1986) and found to be normal, thus justifying the use of the percentile method. The statistical significance of the difference $RPN_{i',k} - RPN_{i,k}$ then was evaluated by the following criteria. If the 95% confidence interval for the difference did not include zero, then the null hypothesis was rejected, the annual change in the RPN was considered statistically significant, and the change in sablefish abundance was considered real. Conversely, if the 95% confidence interval for the difference included zero, the null hypothesis was accepted and the change in sablefish abundance was not considered significant.

RESULTS

The RPN for the Gulf of Alaska increased 111% from 1979 to 1986 (Fig. 3). The 95% confidence interval for this increase did not include zero and therefore was judged statistically significant (alpha = 0.05; Table 3), showing that the difference was not due to random error in the survey and that sablefish abundance in the Gulf of Alaska has increased markedly since 1979. The difference consists of significant increases from 1980 to 1981, 1981

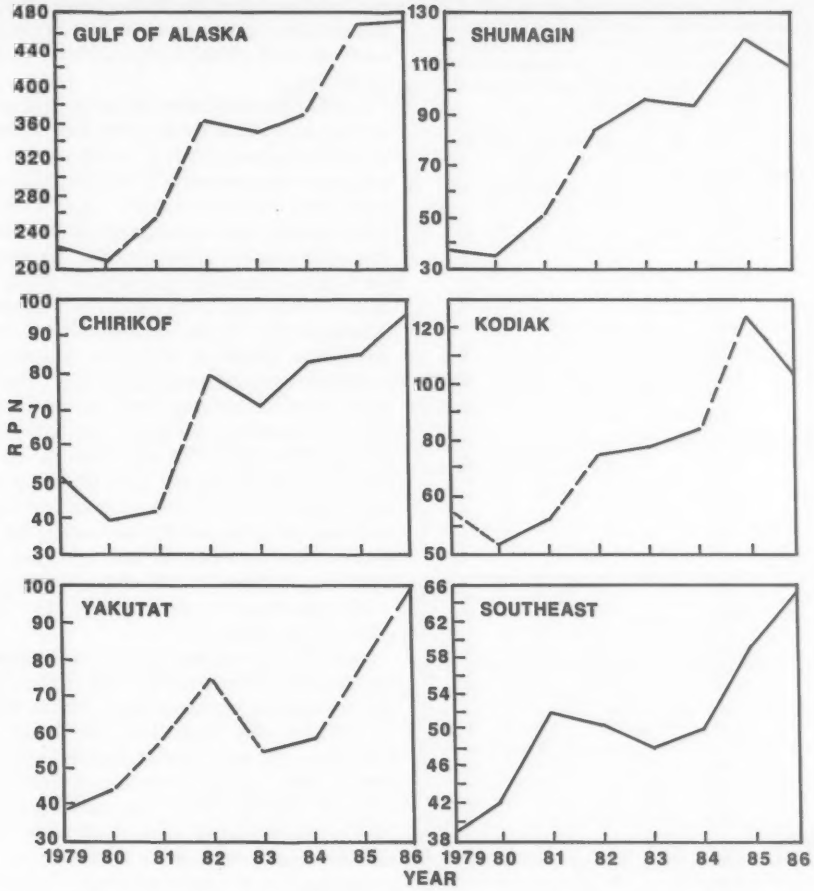

FIGURE 3.—Relative population number (RPN) for the Gulf of Alaska and the Shumagin, Chirikof, Kodiak, Yakutat, and Southeastern areas, 1979–86. Dashed lines (---) signify that the annual change was statistically significant.

to 1982, and 1984 to 1985 (Fig. 3). Differences between other years were not significant.

The RPN for each of the statistical areas of the Gulf of Alaska generally increased from 1979 to 1986 (Fig. 3); the differences between 1979 and 1986 were statistically significant for all areas (Table 3), showing that sablefish abundance has increased throughout the Gulf of Alaska. The sharp jump in the RPN for the Gulf of Alaska from 1980 to 1982 was caused by significant increases in four areas, Shumagin, Chirikof, Kodiak, and Yakutat. The sharp jump from 1984 to 1985 was caused by significant increases in two areas, Kodiak and Yakutat.

DISCUSSION

As noted earlier, sometimes not all strata were sampled at a station (Table 1). This shortcoming was a consequence of the length of the sampling gear and the topography at a station. At stations where the bottom gradient was slight for all or part of the station, the 16 km of longline gear sometimes was not long enough to sample all strata. As a result, sometimes no stations were sampled within certain strata. For these strata, catch per hachi values were estimated using combined data from the current and previous year's data. The resultant values are esti-

TABLE 3.—Statistical significance of annual changes in relative population number of sablefish, Gulf of Alaska, Japan-U.S. cooperative longline survey, 1979–86. The symbols used are defined as follows: + signifies a significant increase in RPN; − signifies a significant decrease in RPN; O signifies no significant change.

Area	Year	80	81	82	83	84	85	86
Gulf of Alaska	1979	O	+	+	+	+	+	+
	1980		+	+	+	+	+	+
	1981			+	+	+	+	+
	1982				O	O	+	+
	1983					O	+	+
	1984						+	+
	1985							O
Shumagin	1979	O	O	+	+	+	+	+
	1980		O	+	+	+	+	+
	1981			+	+	+	+	+
	1982				O	O	+	+
	1983					O	O	O
	1984						O	O
	1985							O
Chirikof	1979	O	O	+	+	+	+	+
	1980		O	+	+	+	+	+
	1981			+	+	+	+	+
	1982				O	O	O	+
	1983					O	O	+
	1984						O	O
	1985							O
Kodiak	1979	−	O	+	+	+	+	+
	1980		O	+	+	+	+	+
	1981			+	+	+	+	+
	1982				O	O	+	+
	1983					O	+	+
	1984						+	O
	1985							O
Yakutat	1979	O	+	+	+	+	+	+
	1980		+	+	O	+	+	+
	1981			+	O	O	+	+
	1982				−	−	O	+
	1983					O	+	+
	1984						+	+
	1985							+
Southeastern	1979	O	+	+	O	+	+	+
	1980		O	O	O	O	+	+
	1981			O	O	O	O	+
	1982				O	O	O	+
	1983					O	O	+
	1984						O	+
	1985							O

mates of catch per hachi as if the strata had been sampled. Because the estimated values mimic the observed data, the probability of rejecting the null hypothesis is somewhat higher than the nominal value. In general an inaccurate estimate should have a small total effect because catch per hachi values were missing for only 9 of the 320 strata available during the survey (8 years × 5 areas × 9 strata). The only comparison where the estimated catch per hachi values might have caused an incorrect conclusion is the 1984–85 comparison where 7 strata were unsampled. This comparison was retested using only the observed catch per hachi values. The annual change, like the comparison using the estimated catch per hachi values, was found to be statistically significant.

Another potential effect of incomplete sampling at a station is bias in the bootstrap calculation. Each bootstrap replicate $RPN_{i,k}^*$ was computed from a bootstrap sample selected by sampling with replacement from the stations within an area. If one or more stations were missing an observation for a strata, then it was possible for the bootstrap sample to have all missing values for the strata. In this case, no catch per hachi values were available to calculate a value for the strata and the value for the strata was treated as zero. This treatment may negatively bias the resultant $RPN_{i,k}^*$. The extent of the negative bias was tested by comparing the RPN to a bootstrap estimate of the RPN, denoted RPN_b, where RPN_b is the mean of the 1,000 $RPN_{i,k}^*$ from an area and year. If RPN_b generally was smaller than RPN, then the bootstrap replicates were negatively biased. The percentage difference between the resultant RPN_b's compared to the RPN's ranged from −0.7 to +0.5 and averaged only +0.03, showing that the negative bias had little effect on the $RPN_{i,k}^*$.

Other fishery and survey data substantiate the significance of the overall increase in the RPN and also the marked increases from 1981 to 1982 and from 1984 to 1985. The CPUE in the Japanese longline fishery showed a similar pattern to the RPN's for the years the data overlapped, from 1979 to 1983; the fishery CPUE increased from the late 1970's, with the largest increase from 1981 to 1982, and decreased from 1982 to 1983 (Fig. 4).

Examination of length compositions for depths 101–200 m indicate that the strong 1977 year class (Sasaki 1982; McFarlane and Beamish 1983; Funk and Bracken 1984) was responsible for the RPN increase from 1980 to 1982 and that the RPN increase from 1984 to 1985 was due to a strong 1980 year class. Sablefish recruiting to the survey area first appear at depths 101–200 m, and strong year classes are more distinguishable in the length compositions at these depths. The length compositions for depths 101–200 m show the initial appearance and subsequent increase in length of fish of the strong 1977 year class (Fig. 5). The mode at 47 cm FL in 1979 indicates the first year that the 1977 year class was available to the survey gear. The rightward movement of the mode in succeeding years illustrates the increase in fish length for the 1977 year class. The movement of the mode slowed in 1982 which we interpret to be due mainly to the movement of larger

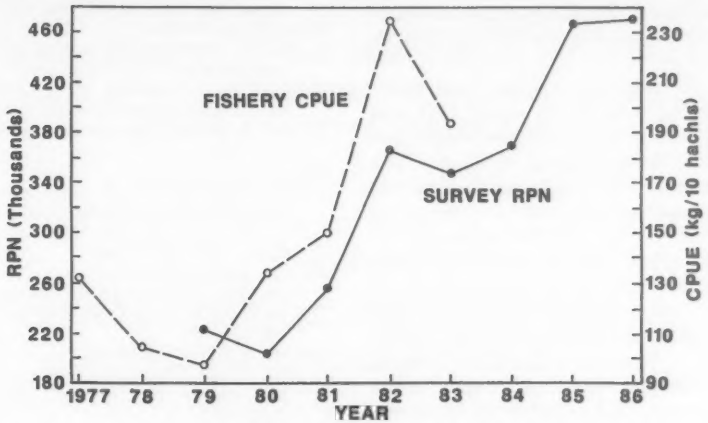

FIGURE 4.—Sablefish catch per hachi (kg/10 hachis) for the Japanese longline fishery, 1977–83 (Fujioka 1986) and relative population number (RPN), 1979–86.

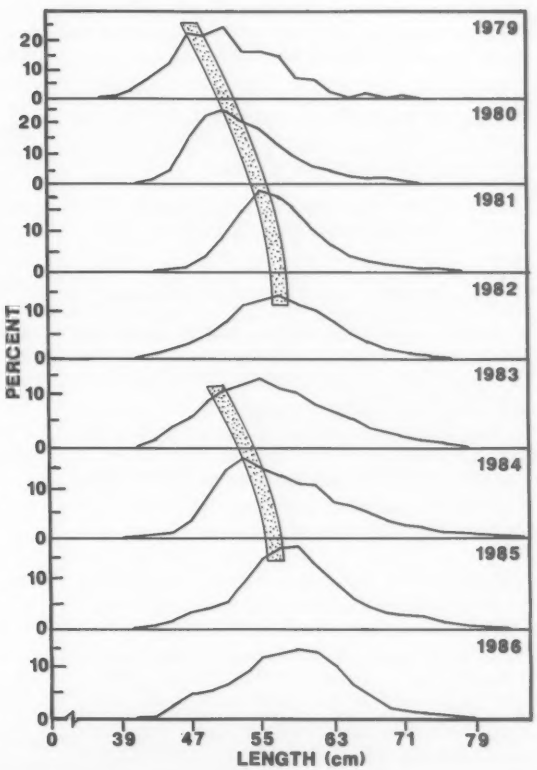

FIGURE 5.—Length-frequency distributions of sablefish in the Gulf of Alaska for depths 101–200 m, 1979–86. The shaded bands illustrate the progression of the modes of two strong year classes, 1977 and 1980.

fish to depths >200 m. The timing of this movement corresponds to the year that the RPN significantly increased.

The pattern of length compositions from 1983 to 1985 parallels those due to the strong 1977 year class and suggests that the 1980 year class is also strong (Fig. 5). The shoulder at 49–51 cm FL in 1983, not present in 1982, indicates the first year that the 1980 year class was available to the survey gear. This shoulder is due to distinct modes at 47–51 cm FL in the Chirikof, Yakutat, and Southeastern areas. The rightward movement of the mode in succeeding years illustrates the increase in fish length for the 1980 year class. The mode at 53 cm FL in 1984 is similar to the modes at 50–57 cm FL found in the Gulf of Alaska for depths 101–200 m during a trawl survey conducted in 1984 by the Northwest and Alaska Fisheries Center (Brown 1986) and is further evidence for a strong 1980 year class. The rightward movement of the mode slowed in 1985, presumably due to movement of larger fish to depths >200 m, and again corresponds to the year of a significant increase in RPN.

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PELAGIC BIOGEOGRAPHY OF THE ARMORHEAD, *PSEUDOPENTACEROS WHEELERI*, AND RECRUITMENT TO ISOLATED SEAMOUNTS IN THE NORTH PACIFIC OCEAN

GEORGE W. BOEHLERT[1] AND TAKASHI SASAKI[2]

ABSTRACT

The pelagic armorhead, *Pseudopentaceros wheeleri*, occurs widely in the North Pacific Ocean. Benthic specimens have been taken from Japan, the Hawaiian Archipelago, and the west coast of North America, but the main reproductive populations are located on southern Emperor-northern Hawaiian Ridge seamounts between lat. 29° and 35°N. The period between spawning and recruitment to the seamounts is apparently between 1.5 and 2.5 years, suggesting an extended pelagic existence. We describe the distributional patterns in the North Pacific based upon over 30 years of published and unpublished records. The majority of pelagic specimens are captured in the subarctic water mass in the northeast Pacific. Based upon the distributional patterns and the oceanography of the North Pacific, we propose migratory paths for both the main population and for the individuals that occur rarely in other locations. The long pelagic period and variability in ocean conditions may play an important role in recruitment to seamounts and the variability in year-class strength for this species.

The pelagic armorhead, *Pseudopentaceros wheeleri*, is a member of the boarfish family Pentacerotidae. Until recently, considerable confusion existed about its taxonomy and distribution. Originally described as *Pentaceros richardsoni* Smith 1844, it was thought to be distributed virtually worldwide, with centers of abundance in the North Pacific and in the South Atlantic near South Africa (Fujii 1986). Occurrences were typically sporadic; most records were from pelagic captures, hence the name pelagic armorhead. Several authors, including Welander et al. (1957), Clemens and Wilby (1961), and Wagner and Bond (1961), used the name *Pseudopentaceros richardsoni*, but more recent studies used the original binomial following Follett and Dempster (1963).

The 1967 discovery of large concentrations of armorhead in the mid-Pacific, over southern Emperor-northern Hawaiian Ridge (SE-NHR) seamounts (from lat. 29° to 35°N) (Sasaki 1974; Uchida and Tagami 1984) stimulated increased interest in this species. Over the next 10 years, nearly 1 million metric tons (t) were taken by Soviet and Japanese trawlers (Borets 1975; Takahashi and Sasaki 1977). The increased availability of specimens allowed Hardy (1983) to revise the family. He first separated the *Pentaceros richardsoni* complex from other members of the genus by referring it to *Pseudopentaceros* Bleeker, based on morphological considerations. Second, he separated the complex into three species: *P. richardsoni* confined to the Southern Hemisphere, and *P. wheeleri* and *P. pectoralis* in the North Pacific. The features used to distinguish *P. wheeleri* and *P. pectoralis* were largely morphological. *Pseudopentaceros pectoralis* is more robust and deeper bodied and its distribution is typically pelagic; *P. wheeleri* was known only from benthic specimens on seamounts. Hardy (1983), however, lacked transitional specimens; subsequent work based on morphological and electrophoretic grounds revealed that *P. wheeleri* was a morphological derivative of *P. pectoralis*, with changes occurring after settlement. The deeper bodied pelagic form ceases growth in length after recruiting to the seamounts and instead transforms body shape to a leaner form. "Fat" and "lean" specimens of the same length thus differ significantly in appearance (Humphreys et al. in press).

Pseudopentaceros wheeleri has an unusual life history. Spawning occurs at the benthic population centers at the SE-NHR seamounts between November and March (Sasaki 1974; Borets 1976; Bilim et al. 1978). Larvae and juveniles are pelagic (Honma and Mizusawa 1969; Fedosova and Komrokov 1975; Borets and Sokolovsky 1978) and widely distributed in the North Pacific. Recruitment to the seamounts

[1]Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396.

[2]Far Seas Fisheries Research Laboratory, 5-7-1 Orido, Shimizu, Shizuoka 424, Japan.

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occurs between ages 1.5 and 2.5 years, but in the major spawning population centers, over 95% of the fish are <2 years (Uchiyama and Sampaga[3]). This lack of older specimens and presence of fish in poor physiological condition has led to suggestions that this species is semelparous, with death after a single spawning (Humphreys and Tagami 1986; Humphreys et al. in press). The long interval between spawning and recruitment for this species suggests that oceanographic conditions in the North Pacific regulate its distribution (Boehlert 1986).

Published records of the pelagic distribution of *P. wheeleri* are too few and varied to understand its biogeography. In different years, specimens have been caught in the Gulf of Alaska, near the Aleutian Islands, and off the coasts of Japan, Oregon, California, and British Columbia. In this paper, we document the pelagic and benthic occurrences from both published and unpublished accounts, consider this distributional pattern in light of general oceanographic conditions in the North Pacific, propose hypotheses about the migration and recruitment of armorhead to the seamounts of the central North Pacific, and assess interannual variation in abundance and how it may relate to oceanographic variability.

[3]Uchiyama, J. H., and J. Sampaga. In review. Age and growth of the pelagic armorhead, *Pseudopentaceros wheeleri*, at Hancock Seamounts. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396.

MATERIALS

The data sources used include published and unpublished collection records from throughout the North Pacific Ocean. Published records on occurrences in Japan (Abe 1957, 1969; Zama et al. 1977; Okamura et al. 1982), the eastern North Pacific (Welander et al. 1957; Larkins 1964; Honma and Mizusawa 1969; Chikuni 1970; Ignell et al. 1986), and the west coast of North America (Wagner and Bond 1961; Follett and Dempster 1963; Smith 1965) were typically of single or a few specimens. Larger numbers of unpublished collection records were in data from large-scale surveys (Table 1). These data

TABLE 1.—Data bases searched for pelagic armorhead, *Pseudopentaceros wheeleri*, captures excluding single collections and literature reports. Areas and seasons are averages over the years covered.

Data source	Years, season effective	Area	
		Lat. N	Long.
Salmon drift gill-net surveys[1]	1972–86, spring-fall	38°–65°	140°E–166°W
University of Washington (FRI) purse seining, longlining[2]	1956–82, spring-summer	42°–60°	165°E–125°W
Canada salmon longlining[2]	1962–67, spring-summer	42°–54°	120°–145°W
Bureau of Commercial Fisheries salmon gill net[2,3]	1955–71, spring-summer	40°–60°	165°E–125°W
Oshoro Maru salmon gill-net-longline surveys[4]	1963–66, 1968, 1969, 1971, 1974–86, spring-summer	36°–66°	163°E–124°W
Hokusei Maru squid and salmon gill-net surveys[4]	1973–86, summer	18°–58°	141°E–156°W
Japan Marine Fishery Resource Research Center pomfret surveys[5]	1979–82, all months	22°–49°	143°E–124°W
Japanese commercial whaling reports[6]	1952–79, summer	40°–58°	
Pacific Biological Station gill-net surveys[7]	1983, 1985–86, spring-summer	47°–54°	138°–130°W
Taiwan Fisheries Research Institute squid surveys[8]	1986, July-August	38°–46°	153°E–175°W
National Marine Fisheries Service Auke Bay cooperative squid gill-net surveys[9]	1985–86	43°–55°	145°–175°W
Japan Fisheries Agency squid gill-net surveys	1986–87, July-August	36°–47°	150°–165°W

[1]Salmon research data file, North Pacific Ocean, 1972–86. Salmon Division, Far Seas Fisheries Research Laboratory, Shimizu, Japan.
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[3]Larkins 1964.
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[5]Japan Marine Fishery Resourse Research Center 1980, 1983a, 1983b, 1985.
[6]Biological data file of whales in the North Pacific Ocean, 1952–79. Whale Section, Far Seas Fisheries Research Laboratory, Shimizu, Japan. See also Chikuni (1970).
[7]Sloan 1983; Robinson and Jamieson 1984.
[8]Z. Shyu, Taiwan Fisheries Research Institute, Keelung 20220, Taiwan, pers. commun. May 1987.
[9]Ignell et al. 1986.

are seasonally limited to primarily spring, summer, and early fall months, but cover 1952–87 and provide broad geographic coverage between lat. 18° and 66°N. Greater detail and a summary of many of these surveys are provided by Macy et al. (1978). Since armorhead were an incidental catch, it is difficult to assess the relative value of the different surveys with respect to sampling effort.

The most typical sampling gears used were longlines, gill nets, and purse seines targeting salmon, squid, or pomfret; rarer collections were made with plankton nets, dip nets, or hook and line. Thus, sampling was typically in surface waters, most likely in the upper 50 m; the true depth distribution of the pelagic animals, however, is unknown. The only other "gear" was the sei whale, *Balaenoptera borealis*, from which stomach contents were studied for about 27 years; Chikuni (1970) reported armorhead in the stomachs.

RESULTS AND DISCUSSION

Distributional Patterns

The known center of distribution and spawning for benthic *P. wheeleri* is in the SE-NHR seamount region, bounded by lat. 29°–35°N and long. 171°E–179°W (Takahashi and Sasaki 1977; Humphreys and Tagami 1986). These reproductive fish are typically between 23.0 and 28.5 standard length (SL) (Sasaki 1986) and range in age from 1.5 to 2.5 years (Uchiyama and Sampaga fn. 3). They are found at depths between 200 and 500 m (Takahashi and Sasaki 1977). Other benthic occurrences have been recorded but are sporadic (Fig. 1). Several specimens were captured off Japan in 1957 (Abe 1957), 1969, 1971–73, 1976 (Zama et al. 1977), and 1979 (Okamura et al. 1982). These fish were typically the same size as those captured on the seamounts, but no mention of reproductive status was made. Fish of similar length occur rarely on the west coast of North America, but only between lat. 37°00′ and 44°25′N (Wagner and Bond 1961; Follett and Dempster 1963; Smith 1965). Again, reproductive status is unknown for these specimens. No benthic occurrences off British Columbia or Alaska have been reported, despite extensive trawling surveys which included seamounts (Hughes 1981; Alton 1986). Large specimens have been taken rarely in the Hawaiian Archipelago (Fig. 1; Randall 1980; Humphreys et al. in press) and are typically 4–5 years old and appear to be in reproductive condi-

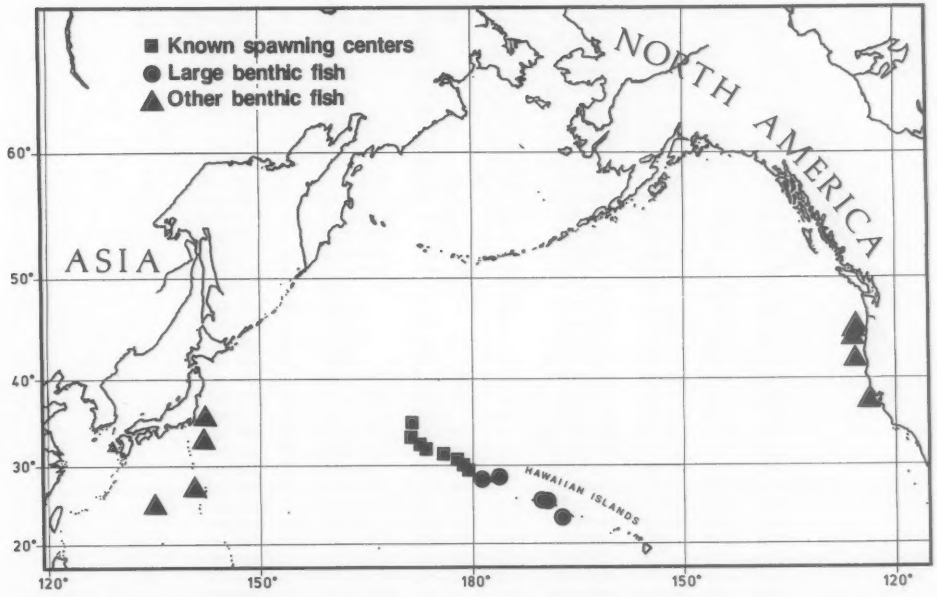

FIGURE 1.—Known distribution of benthic occurrences of pelagic armorhead, *Pseudopentaceros wheeleri*. Squares represent the main population centers at central North Pacific seamounts. All others are rare or sporadic occurrences.

tion. Their relationship with the SE-NHR seamount populations is unknown.

The most common pelagic occurrences (1955–87) were fish ranging from 18 to 26 cm SL; smaller sizes are poorly represented, probably because of the nature of the sampling gear. Smaller specimens were generally captured with plankton nets (Fedosova and Komrakov 1975; Borets and Sokolovsky 1978), dip nets (Honma and Mizusawa 1969; Randall 1980; Fujii[4]), and in one case, in a whale stomach (Kawamura 1982). The sea-surface temperatures at which the specimens were captured ranged from 8.6° to 15.0°C (average 12.1°C). For all years, pelagic captures were restricted to the eastern North Pacific, with the exceptions of larvae or early juveniles captured near the spawning centers at the seamounts (Komrakov 1970; Table 2), over 20 specimens in a Bryde's whale stomach in 1979 (Kato[5], Fig. 2B), and two individuals captured in 1986 at long. 155°E (Fig. 2). This is despite extensive sampling in the western North Pacific, particularly by the Japan Marine Fishery Resource Research Center (JAMARC) and the Hokkaido University, and in the Bering or Okhotsk Seas (Table 1).

Pelagic captures in the 1950's were sporadic, but several fish were taken north of lat. 50°N, especially in 1958 (Fig. 2A). Relatively few were captured in the 1960's, with the exception of July through early August 1969, when the armorhead was an impor-

[4]E. Fujii, Nippon Luther Shingaku Daigaku, Tokyo, Japan, pers. commun. July 1987.

[5]H. Kato, Whales Research Institute, Tokyo, Japan, pers. commun. December 1987.

TABLE 2.—Pelagic specimens of armorhead, *Pseudopentaceros wheeleri*, for which sizes were available. The growth curve from Uchiyama and Sampaga (text footnote 3), based upon enumeration of daily growth increments, was used to deduce age from length. For the youngest fish (bottom), average readings from daily growth increments, rather than the growth curve, were used. Data are from various published sources and collections listed in Table 1. (SST = sea-surface temperature.)

Year	Date	Lat. N	Long.	SST	Standard length (mm)	Age (yr)	No.	Gear
1955	9/27	45°41′	165°5′W	—	108–122	0.38–0.42	2	Gill net
1955	9/27	45°35′	165°5′W	—	200	0.79	1	Dip net
1956	7/31	45°49′	160°3′W	12.2	245	1.29	1	Gill net
1956	9/15	45°00′	155°00′W	12.1	245	1.29	2	Gill net
1956	9/17	49°00′	150°00′W	13.2	245	1.29	1	Gill net
1956	9/17	51°00′	150°00′W	11.0	245	1.29	1	Gill net
1958	8/14	44°39′	174°48′W	—	64–91	0.26–0.33	2	Dip net
1958	8/25	49°43′	146°10′W	11.8	256	1.50	1	Gill net
1963	8/24	49°0′	162°0′W	12.9	249	1.40	1	Gill net
1967	6/15	54°38′	150°1′W	8.8	121–134	0.42–0.46	4	Dip net
1968	7/	41°30′	165°30′W	—	285	>2.00	1	Handline
1969	4/1	29°48′	179°5′E	—	8–23	0.08–0.25	?	Plankton
1969	4/1	31°6′	176°0′E	—	8–23	0.08–0.25	—	Plankton
1969	4/1	32°6′	173°0′E	—	8–23	0.08–0.25	—	Plankton
1972	5/21	38°30′	175°3′W	14.3	42–50	0.21–0.23	5	Whale stomach
1984	7/25	45°30′	155°0′W	13.0	262–265	1.81–2.02	3	Gill net
1984	7/25	45°26′	154°58′W	12.0	278	>2.00	2	Longline
1985	7/9	46°57′	129°4′W	—	272	>2.00	1	Gill net
1985	7/10	47°30′	128°36′W	—	272–298	>2.00	2	Gill net
1985	7/11	47°59′	129°19′W	—	277	>2.00	1	Gill net
1985	7/13	46°23′	131°29′W	—	188–219	0.71–0.94	5	Gill net
1985	7/14	46°40′	131°8′W	—	183–233	0.68–1.1	9	Gill net
1985	7/15	46°35′	131°5′W	—	206	0.83	1	Gill net
1985	7/19	46°54′	131°28′W	—	190–217	0.72–0.92	2	Gill net
1985	7/21	47°18′	130°23′W	—	191–220	0.73–0.95	3	Gill net
1985	7/22	47°35′	130°48′W	—	190–201	0.72–0.79	2	Gill net
1985	7/23	47°37′	130°31′W	—	198–200	0.77–0.79	2	Gill net
1985	7/12	47°0′	155°1′W	11.6	263–265	1.87–2.02	2	Longline
1985	7/13	45°28′	155°5′W	11.8	238–262	1.17–1.81	12	Longline
1985	7/11	47°0′	155°0′W	11.6	248–262	1.35–1.81	5	Gill net
1985	7/12	45°30′	155°0′W	11.8	235–240	1.12–1.20	4	Gill net
1985	7/13	44°0′	155°0′W	12.8	248–258	1.35–1.63	4	Gill net
1985	2/23	30°16′	181°18′W	—	8–15	0.08–0.16	15	Neuston
1985	2/24	29°27′	180°56′W	—	5–15	0.04–0.16	15	Neuston
1986	8/3	43°51′	164°54′W	13.0	50–100	0.23–0.35	5	Dip net

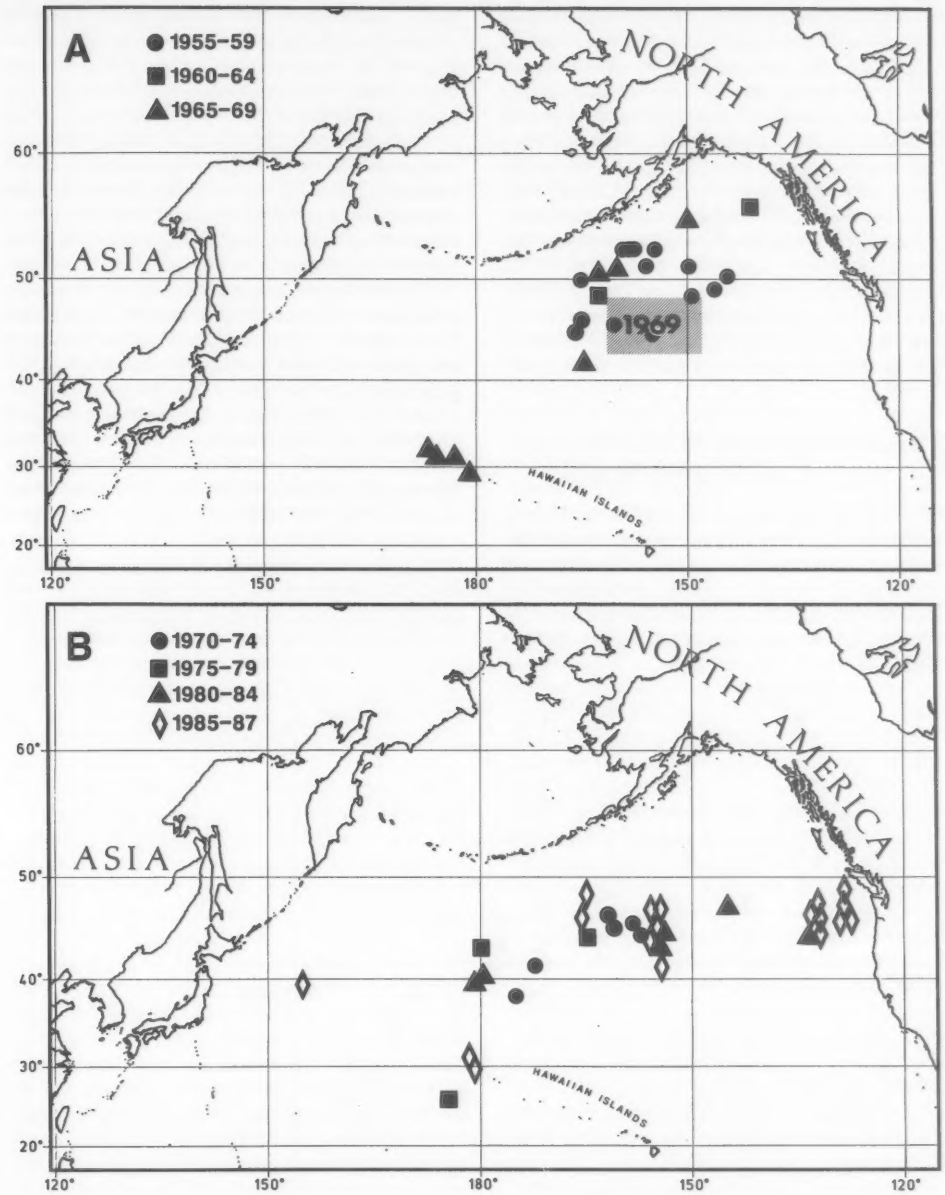

FIGURE 2.—Records of pelagic occurrences of armorhead, *Pseudopentaceros wheeleri*, in the North Pacific. Most data were obtained from either published records or unpublished data described in Table 1: Each symbol represents a collection taking armorhead, rather than single specimens. (A) 1955–69. Here, note that the area in the box contains the locations of 195 sei whales captured in July–August 1969 that had fed extensively upon armorhead. The samples from the central Pacific were larvae and early juveniles (Fedosova and Komrakov 1975). (B) 1970–87.

tant diet component of sei whales taken by the Japanese commercial fleet. This species normally feeds on zooplankton and micronekton (Kawamura 1982), but in this year, 195 whales were recorded to have fed extensively on armorhead. Although data records for whale stomach contents extend from 1952 to 1979, 1969 was the only year when large numbers fed on armorhead, with the exception of two occurrences each in 1971 and 1972. Based on the known feeding mode of sei whales, Chikuni (1970) suggested that the armorhead apparently schools in surface waters. In the 1970's, catches were relatively small, but in the 1980's, specimens have been captured in each year, with the greatest catches in 1985. In that year, fish occurred in more easterly areas as compared to other years.

Relationship of Distribution Patterns to North Pacific Oceanography

The SE-NHR seamounts are located in the mid-Pacific transition zone, between subarctic and subtropical water masses (Roden 1970). The spawning season of armorhead typically lasts from late November through March (Sasaki 1974; Bilim et al. 1978), and larvae are neustonic, at least through the first few months of life (G. W. Boehlert unpubl. data). Near surface drift in this region is largely wind driven (McNally 1981); as shown by Lagrangian drifters, mean surface flow in the SE-NHR seamount region during winter months is typically eastward (Kirwan et al. 1978; Emery et al. 1985) or southeastward (McNally et al. 1983), and long-term mean Ekman transport has a southeastward component (Favorite et al. 1976). Based on mean ship-drift data, progressive vector diagrams over a 3-mo period, with starting points at four SE-NHR seamounts (Bakun[6]), show this typical eastward flow with a southward component (Fig. 3). If pelagic armorhead followed such a pattern, individuals would remain in the subtropical gyre, continuing eastward and then turning south, entering the California Current system. The scarcity of specimens in this region (Figs. 1, 2) suggests instead that most fish move northeastward in some manner, entering subarctic waters and residing within the Alaska gyre; surface drift in winter is northeastward in anomalous years (McNally 1981), and average

[6]Compilation by the NMFS Pacific Fisheries Environmental Group from historic ship drift files assembled by the U.S. Naval Oceanographic Office (A. Bakun, Pacific Fisheries Environmental Group, National Marine Fisheries Service, NOAA, P.O. Box 831, Monterey, CA 93942, pers. commun. April 1987.

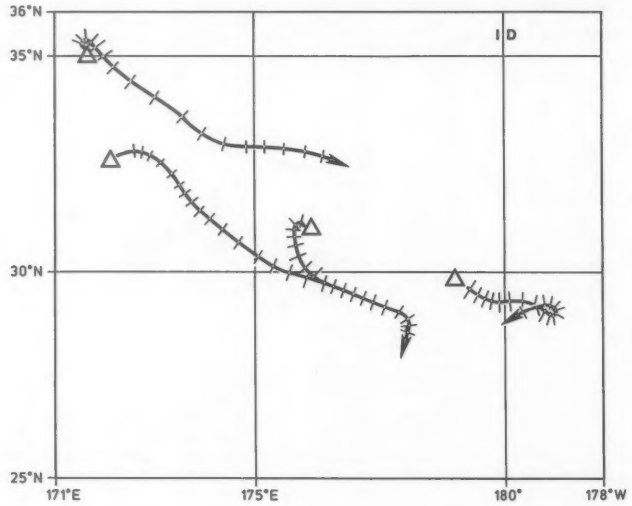

FIGURE 3.—Progressive vector diagrams of mean surface currents (starting date, 15 December; duration, 90 days), from long-term mean ship drift data from 1° squares, with distances calculated on a daily basis. Triangles indicate starting locations at four seamounts with armorhead spawning populations. Each mark on the vector between the origin and arrow represents a 5-d period. See text footnote 6.

surface flow is in this direction in summer months (McNally et al. 1983).

The two available studies on larval distribution of armorhead are conflicting and suggest that patterns of movement may differ from year to year. Komrakov (1970) conducted surveys in March–April 1969 and observed larvae only at northern seamounts and in the open ocean several hundred kilometers northeast of the SE-NHR seamounts. Borets (1979), however, observed 5–20 mm larvae remaining mostly around the seamounts, with highest abundance south of lat. 33°N in 1976. Because spawning occurs at seamounts northwest of this area, this pattern is consistent with southeastward drift during the first few months of life (Fig. 3). If larvae remain in the seamount region, they could be transported to the northeast in summer months, or they may actively migrate northeastward after reaching the juvenile stage. A similar migration apparently occurs for the pomfret, *Brama japonica*, which prior to spawning moves into the North Pacific current region in a broad latitudinal band between the subtropical convergence and the subarctic boundary; immature fish and spent adults then move northward into the subarctic region to feed during April–May (Shimazaki and Nakamura 1981). The pomfret differs from the armorhead, however, in that it remains pelagic throughout its life and also is abundant in the western North Pacific. Larval and juvenile *Brama* sp. do occur in the same area as larval armorhead (Borets and Sokolovsky 1978; G. W. Boehlert unpubl. data).

A possible scenario of movements after the larval stage can be deduced from the ages of individuals captured in different regions. Based upon the growth of pelagic armorhead (Uchiyama and Sampaga fn. 3), most of the larger specimens indicated in Figure 2 are from 1 to 2 years old, and the pelagic duration for this species is most often from 1.5 to 2.5 years. Using daily growth increments for larval and small juveniles and fitted growth curves for larger juveniles and adults, one can convert lengths to ages. The pelagic specimens of known length range in estimated age from 0.04 to >2 years (Table 2). The youngest animals are typically found in the region of the seamounts (Komrakov 1970; Fedosova and Komrakov 1975; Borets and Sokolovsky 1978), but intermediate-sized fish are found north and east of the seamounts. Different age groups seem to be distributed in different areas in the eastern North Pacific (Fig. 4). Armorhead spawn in the seamount region (as area A in Figure 4) during November to March, and juveniles 5–25 mm long are found in the SE-NHR seamounts area from February to early April (Fedosova and Komrakov 1975; Borets 1979). Subsequent occurrences of fish older than 0.25 year (Table 2) are found only in the region northeast of the seamounts and in the Gulf of Alaska (area B in Figure 4). Northeastward movements are contrary to mean ocean currents, but Roden et al. (1982) described intense northward flow along the axis of the southern Emperor Seamounts that could conceivably play a role in transport of fish at the youngest stages.

Recruitment of later stage armorhead to the seamounts requires movement to the west. The only significant westward circulation in the North Pacific is found in the Alaskan Stream (Favorite 1967). This narrow current occurs north of lat. 51°N and extends westerly to near long. 170°E, where it splits to two branches, one turning northerly into the Bering Sea and the other southerly under the influence of the northern Emperor Seamounts or Kormandorskie Ridge (Favorite 1967; dashed line in Figure 4). Darnitsky et al. (1984) described southerly movement of this water to at least lat. 40°N and suggested that it played a role in transport of planktonic food for armorhead on the seamounts. Unless returning armorhead are deep in the water column and therefore not sampled, distributional data (Fig. 2) do not support this route for westerly movement. Fish near recruitment size and age are instead captured in the region marked C on Figure 4, south of the area where younger fish are captured. These fish apparently migrate back to the region of the seamounts by some unknown, but probably active, mechanism.

Two less important, but plausible, movement patterns may explain the rarer occurrences in southern Japan, off Oregon and California, and in the Hawaiian Archipelago (Fig. 4). Chelton (1984) discussed possible interannual changes in the latitudinal position of the West Wind Drift which may lead to differing magnitudes of transport in the Alaska and California Currents. The rare benthic occurrences of the pelagic armorhead off the west coast of North America (area D in Figure 4) may come from specimens that drift southward in the California Current in years of greater southern transport. Some of these may not settle out and remain within the subtropical gyre, possibly recruiting to the Hawaiian chain far to the south of the normal reproductive population. This route, because of its distance, apparently takes considerably longer than that in the subarctic gyre; based upon satellite drifters, McNally et al. (1983) suggested that a full circuit of the subtropical gyre takes 4.5 years. The armorhead collected in the Northwestern Hawaiian

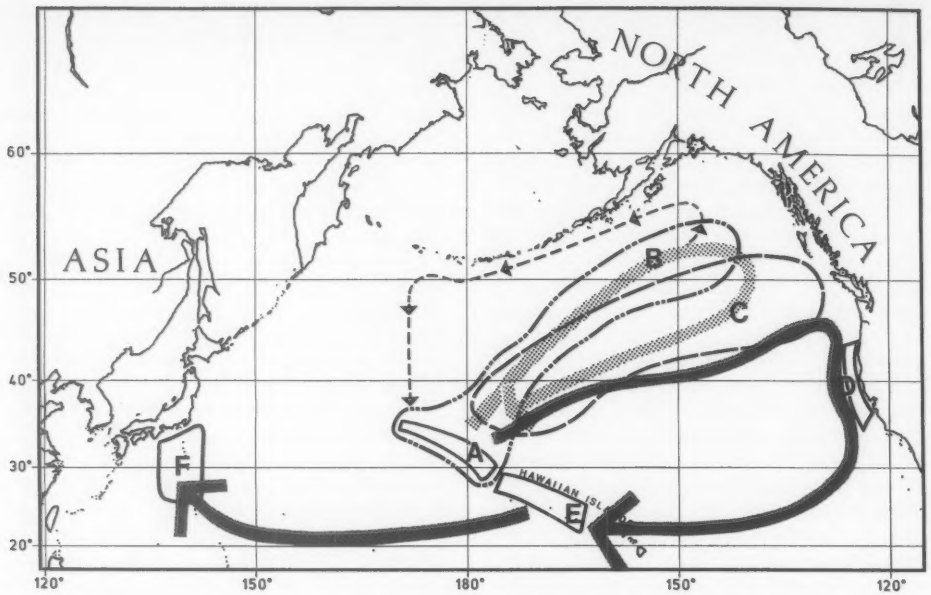

FIGURE 4.—Distributions of benthic and pelagic specimens of armorhead, *Pseudopentaceros wheeleri*, by age group with possible patterns of movement. Area A represents the major spawning area, and area E the region inhabited by the large, older specimens. Area B is the region in which specimens younger than 1 year have been captured, and area C where fish from 1 to 2 years old have been captured. The arrow through this region represents the main population movement pattern. Other arrows represent possible movements for stray fish. Areas marked D and F represent locations of benthic collections from California and Japan, respectively.

Islands (area E in Figure 4) are typically larger than those in the normal part of the range and are correspondingly older, with ages estimated at 4 or 5 years (Humphreys et al. in press), similar to the time suggested for a circuit of the gyre by McNally et al. (1983).

The other plausible movement pattern can be used to explain the existence of specimens in Japan. Benthic specimens of armorhead are rarely captured in Japan (Fig. 1); a report of 3,000 t landed in 1969 by Soviet fishermen in this region (Abe 1969) may be in error, since the Soviet fishery on the SE-NHR seamounts developed heavily that year (Borets 1975) and SE-NHR fish were likely sold in Japan. The reproductive condition of these animals is not known, so the source of the spawning population supplying them is at question. The large, reproductive individuals in area E (Fig. 4) have been found as far south as lat. 23°43′N (Humphreys et al. in press). It is possible that larvae and juveniles are transported to Japan in the northern part of the North Equatorial Current (Uda and Hasunuma 1969). This is consistent with the capture of over 20 fish in a Bryde's whale stomach in September 1979 at lat. 26°N (H. Kato fn. 5; Fig. 2B). Subsequent captures of this species have not been made in Japanese waters, where their presence may require a rare recruitment event from an upstream population source, as has been suggested for seamount populations of lobsters (Lutjeharms and Heydorn 1981). These animals may also remain within a gyral circulation, however, as suggested by the presence of two specimens captured in the Kuroshio in 1986 (Fig. 2B).

Recruitment to the Seamounts

The seasonal timing of the recruitment of the pelagic armorhead to the SE-NHR seamounts is unknown. That no records of larger pelagic fish captured near the seamounts (Fig. 2) exist may be an artifact of sampling in inappropriate seasons or lack of sampling in deeper water. The youngest benthic specimens from the seamounts were slightly in ex-

cess of 1.5 years in early summer (Uchiyama and Sampaga fn. 3) and 2 years in winter, suggesting that some recruitment occurs in spring.

In most fisheries, temporal recruitment patterns can be discerned from length-frequency analyses, because the smaller recruits represent a larger proportion of the population during the season of recruitment. For the armorhead, no increase in smaller size classes is apparent in monthly length-frequency samples. This may be due to cessation of somatic growth after recruitment to the seamount (Humphreys and Tagami 1986; Uchiyama and Sampaga fn. 3). Early recruits, with their deeper bodies and greater fat content, differ morphologically from longer seamount residents. The transition from so-called "fat" to "lean" morphotypes occurs in association with development of gonads (Humphreys et al. in press). Thus, an index of morphological change can be used to detect recruitment patterns, much the same as length frequencies can be used for other species. Condition factor is frequently used to assess "fatness" of fish; it is normally expressed as weight divided by length to a power (typically 3) multiplied by some scaling factor (Ricker 1975). For armorhead, there is a marked change in condition factor with morphological change; newly recruiting fish have high condition factors relative to intermediate or lean fish. By considering the monthly proportion of fish above an arbitrary value of condition factor, we can estimate the influx of new recruits to the seamounts. During May 1972–December 1973, the major influx of new recruits with a high condition factor occurred in April–May 1973 (Fig. 5). The data for 1972 are incomplete, but some recruitment apparently occurred in August and September (Fig. 5). Differences in seasonality of recruitment between 1972 and 1973 may be indicative of interannual variability in temporal recruitment patterns.

An influx of fish to the seamounts may also be reflected in the catch per unit effort (CPUE), an index of stock abundance. Monthly averages of CPUE (in metric tons per hour) by Japanese trawlers for armorhead at the SE-NHR seamounts were highest in March and April (Sasaki 1986). Overall armorhead CPUE decreased continuously from 54.1 t/h in 1972 to only 0.3 t/h in 1982 (Sasaki 1986) and further decreased to 0.06–0.07 t/h in 1983–85 (T. Sasaki unpubl. data). The estimated CPUE in 1986, however, was 0.31 t/h, an increase of four or five times that in the previous year. The CPUE of trawlers operating in May–September 1986 was highest in May, decreased in June and July, but increased slightly in August and Septem-

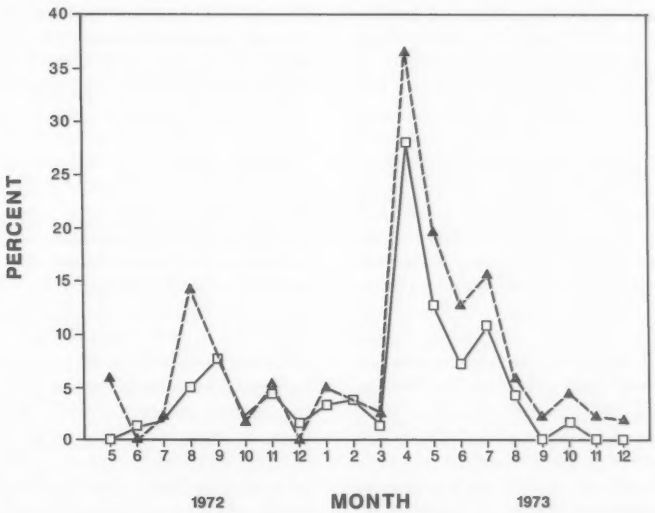

FIGURE 5.—Seasonality of the proportion of armorhead, *Pseudopentaceros wheeleri*, with condition factors ≥2.0 from four seamounts of the northern Hawaiian Ridge (Southeast Hancock, Northwest Hancock, C-H, and Colahan) for 1972–73. Squares, males; triangles, females. Data are based upon 2,104 males and 1,704 females.

ber. Based on all the information, the major recruitment may occur in spring with some additional recruitment in August and September (Fig. 5); data are not sufficient to determine the recruitment pattern in detail.

A broad geographic separation exists between the location of pelagic captures of larger armorhead and the location of the spawning populations (Figs. 2, 4). If recruitment to the seamounts occurs predominantly in spring (as suggested for 1973 in Figure 5), then temporal sampling patterns may have missed these fish, although JAMARC pomfret surveys covered this area in some seasons (Table 1). Locating the seamounts, which have small (2–5 km) summits must be a formidable task given the wide ocean areas over which armorhead are distributed. A similar situation exists for rock lobster, *Jasus tristani*, in the South Atlantic, that recruits from an upstream population some 2,000 km away and in sufficient numbers to support a fishery on Vema Seamount in some years (Lutjeharms and Heydorn 1981).

Open-ocean migrations of fishes may depend upon many potential cues, including electric fields (McCleave and Power 1978), magnetic fields (Walker 1984), gyres (Williams 1972), and pheromones (Nordeng 1977). Certain characteristics of these isolated, open-ocean seamounts may promote their detection by armorhead. First, current-topography interactions may create significant signals in physical and biological features. The region of the SE-NHR seamounts is active in front development (Roden and Paskausky 1978); upwelling, eddies, and other aspects of flow complexity also occur around these seamounts (Roden et al. 1982) and downstream from them (Royer 1978). The biological signals may include increased chlorophyll in response to upwelling or doming of isotherms (Genin and Boehlert 1985), or aggregations of various organisms and the larger animals which prey upon them around seamounts (see review in Boehlert and Genin 1987). Gravity anomalies associated with seamounts may also play a role; positive gravity anomalies exist at the summit and slopes, and negative anomalies are seen in the surrounding "moat" regions (Wedgeworth and Kellogg 1987). Seamounts often have strong magnetic dipoles associated with them, and the dipole might serve as a landmark for magnetic orientation by fish (Klimley[7]). While fish have been shown to have magnetoreceptors (Walker et al. 1985), their use of magnetic maps remains speculative but possible (Gould 1985). Although we cannot postulate the mechanism that armorhead use for recruitment, it is clear that the effects of seamounts may be detected at distances greater than their area alone would suggest.

[7]P. Klimley, Scripps Institution of Oceanography, La Jolla, CA 92038, pers. commun. 30 June 1987.

Interannual Variations in Recruitment Strength

The year-class strength of armorhead recruiting to seamounts appears to be independent of the parent stock size (Wetherall and Yong 1986). As an example, Borets (1975) estimated that on the SE-NHR seamounts from 1968 to 1973, the stock size varied by a factor of <1.8 while recruitment varied by >5.5 times. The relative abundance of armorhead at the SE-NHR seamounts area increased in 1986 after a long period at a very low level. This increase probably corresponds to the high abundance of pelagic specimens captured in the northeastern Pacific in 1985 (Fig. 2B; Table 2) that consisted of two age groups. The increased recruitment at the SE-NHR seamounts in 1986 suggests that environmental conditions were favorable to the survival of young armorhead in the 1984 and 1985 winter seasons.

A wide variety of factors, both biotic and physical, can affect survival and ultimate year-class strength in fishes (Lasker 1978). During the 2 years between spawning and recruitment for armorhead, an extended migration through varied pelagic environments occurs (Fig. 4). Feeding conditions for larval and juvenile stages are characterized by interannual variability; Fedosova (1980) suggested that warm years were more productive for zooplankton prey and, thus, favorable to the survival of young armorhead. Interannual variation in atmospheric systems (Seckel 1988) or large-scale ocean currents of the kind described by Mysak et al. (1982) may also play a role in armorhead recruitment strength. Changes in the position of the Alaska gyre by up to 700 km southwest of its normal position may have occurred from 1981 to 1985, with an associated increase in seawater temperature (Royer and Emery 1987). Large-scale atmospheric phenomena, such as the longitudinal position of the Aleutian Low, may create definite interannual variations in winter wind systems that may be seen in surface current patterns (Seckel 1988). These patterns may, in turn, be related to the latitudinal position of the subtropical front, which varies interannually between lat. 28° and 32°N (Roden 1970). Variability in these features influences surface drift (McNally 1981), which in turn affects the neustonic young of armor-

head. If flow in certain years results in transport of armorhead to other regions (such as the western Pacific or the southern part of the northeast Pacific; Fig. 4), it is possible that large-scale mortalities of armorhead occur later in life, resulting in weak year classes at the SE-NHR seamounts.

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THE TIMING AND SIGNIFICANCE OF DENSITY-DEPENDENT AND DENSITY-INDEPENDENT MORTALITY OF AMERICAN SHAD, *ALOSA SAPIDISSIMA*

THOMAS F. SAVOY AND VICTOR A. CRECCO[1]

ABSTRACT

We used stock-recruitment, pre- and postrecruitment mortality data for American shad, *Alosa sapidissima*, in the Connecticut River to estimate density-dependent and density-independent mortality rates at the prejuvenile (age 1–100 days) and postjuvenile (age 101 days to 5 years) phases. Total postjuvenile mortality rates from 1967 through 1982 were dominated by density-independent mortality, with only 6% ($Z_{D\,post}$ = 0.30) of the mean total (Z = 4.85) being ascribed to density-dependent processes. By contrast, 23% ($Z_{D\,pre}$ = 1.13) of the total prejuvenile mortality was compensatory, of which nearly all took place during the embryonic and early larval periods. Egg and early larval mortality rates from 1979 through 1987 were positively correlated to June river flows, and inversely related to mean June temperature, whereas mortality rates of all other life stages showed no such relationships. Daily egg and early larval mortality rates from 1979 through 1987 were usually higher and more variable than mortality rates during later stages. There were significant negative correlations between egg and early larval mortality rates and the strength of 1979–87 year classes in the adult stock, whereas mortality rates of late larvae and juveniles were independent of year-class strength. Density-dependent mortality during the egg and early larval stages comprised over 40% of the total mortality at those stages, resulting in the number of midlarvae and juveniles being positively correlated to adult recruitment. These data suggest that year-class strength of American shad in the Connecticut River is established after the egg and larval stages.

It is generally accepted that year-class strength of most fishes is established prior to the juvenile stage from density-independent (climatic factors) and density-dependent (competition, predation, cannibalism) processes (Cushing 1974; May 1974; Goodyear 1980). Although density-dependent mortality is believed to be the mechanism that keeps fish populations stable under low to moderate exploitation (McFadden 1977; Cushing 1980), density-dependent processes such as inter- and intraspecific competition, predation, and cannibalism are difficult to measure. This is particularly so for many highly fecund fishes, whose population sizes undergo wide fluctuations that often cannot be predicted by conventional stock-recruitment models (Parrish and MacCall 1978; Bakun 1984). Despite the acknowledged importance of density-dependent mortality to stock-recruitment theory (Ricker 1975; Ware 1980), few studies have been able to quantify density-dependent mortality, or determine the life stages at which compensation occurs.

Density-dependent mortality may be confined to the prejuvenile stage (Cushing 1974, 1980) or the postjuvenile oceanic stage (Peterman 1978, 1982), or may occur throughout the prerecruitment period (Gulland 1965). The testing of these hypotheses has proceeded slowly because of environmental noise surrounding many stock-recruitment relationships, measurement errors associated with recruitment estimates (Ludwig and Walters 1981), and the lack of long-term mortality data on eggs and larvae.

One species, for which accurate and long-term stock-recruitment and prerecruitment mortality data exist, is the American shad, *Alosa sapidissima*, an anadromous clupeid that spawns in many Atlantic coast rivers (Walburg and Nichols 1967). Previous studies on American shad in the Connecticut River have demonstrated that larval and juvenile mortality rates decline with age (Crecco et al. 1983, 1986) and that growth and survival rates among discrete larval cohorts are significantly affected by short-term hydrographic and meteorological events (Crecco and Savoy 1985b, 1987a). Although previous stock-recruitment studies of Connecticut River shad (Leggett 1977; Lorda and Crecco 1987) found evidence of density-dependent mortality before the juvenile stage, no studies have attempted to estimate density-dependent mortality during the egg and larval stages, or quantify density-dependent and

[1]Connecticut Department of Environmental Protection, Marine Fisheries Office, Waterford, CT 06385.

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density-independent mortality after the juvenile stage.

In this study we used stock-recruitment, pre- and postrecruitment mortality data for American shad in the Connecticut River from 1967 through 1987 to 1) estimate egg mortality rates for the 1979–87 year classes; 2) measure the contribution of density-dependent and density-independent mortality before and after the juvenile stage; and 3) determine the life stage(s) at which most of the density-dependent mortality takes place.

METHODS

Data Source

Estimates of adult recruitment and parent stock size (± SE) from 1967 to 1982 (Table 1) were based on annual population estimates derived by earlier mark-recapture studies (Leggett 1976; Crecco and Savoy 1987[2]) and by the annual mean number of American shad lifted over the Holyoke Dam (Crecco and Savoy 1985a). The parent stock size (PAR_t) from 1967 through 1987 was the annual population estimate of female shad minus that year's commercial catch of female shad. Parent stock (PAR_t) was separated into the parent stock that spawned above the Holyoke Dam (P_a) (Moffitt et al. 1982; O'Leary and Booke 1986[3], 1987[4]) and the spawning stock that spawned below the dam ($P_b = PAR_t - P_a$).

Since female American shad mature between ages four and six, female shad recruitment from the 1967–82 year classes was the sum of virgin 4-, 5-, and 6-yr-old female shad in the 1970–87 runs based on the age-class structure from previous studies (Jones et al. 1976; Leggett 1976; Crecco et al. 1984[5]). Since the sex ratio of mature progeny from each year class is close to 1:1 (Leggett 1976), total recruitment (R_t) from the 1967–82 year classes was estimated by doubling the female shad recruitment estimates. Direct estimates of male shad recruitment are biased by gill net selectivity and differential culling practices of commercial fishermen (Crecco et al. 1984[6]).

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[3]O'Leary, J., and H. E. Booke. 1986. Connecticut River anadromous fish investigations. Mass. Coop. Fish. Res. Unit Proj. Performance Rep., F-45-R-2, 37 p.

[4]O'Leary, J., and H. E. Booke. 1987. Connecticut River anadromous fish investigations. Mass. Coop. Fish. Res. Unit Proj. Performance Rep., 32 p.

[5]Crecco, V. A., T. Savoy, and L. Gunn. 1984. Population dynamics studies of American shad in the Connecticut River. CT Dep. Environ. Prot. Final Rep. AFC 13, 76 p.

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TABLE 1.—Estimates of total female American shad parent stock, female spawning stock above and below the Holyoke Dam, mean June flows from 1967 to 1987, and total number of adult recruits from the 1967–82 year classes. SE = standard errors about the estimates × 10^3.

Year	Total spawning stock × 10^3	SE	Spawning stock above × 10^3	SE	Spawning stock below × 10^3	SE	Recruitment × 10^3	SE	June flow m^3/s
1967	167	35	4	0.8	163	34	444	112	437
1968	202	38	5	0.9	197	37	236	59	603
1969	384	70	10	1.8	374	68	490	116	375
1970	413	95	12	2.8	401	92	550	126	243
1971	424	111	14	3.7	410	107	982	205	203
1972	167	40	8	1.9	159	38	430	87	616
1973	111	30	3	0.8	108	29	308	70	534
1974	306	62	10	2.0	296	60	652	139	334
1975	247	65	16	4.2	231	61	560	101	379
1976	435	80	166	31.0	269	49	650	105	286
1977	207	39	112	21.0	95	18	1,240	191	250
1978	210	54	45	12.0	165	42	714	110	488
1979	248	51	87	18.0	161	33	882	127	445
1980	341	58	196	33.0	145	25	1,256	196	201
1981	293	50	143	24.0	150	26	758	132	316
1982	501	67	109	15.0	392	52	282	49	643
1983	423	77	185	34.0	238	43			386
1984	610	67	245	27.0	365	40			661
1985	555	96	219	38.0	336	58			311
1986	392	71	175	32.0	217	39			439
1987	235	37	136	14.0	146	23			250

American shad larvae (10–30 mm TL) were sampled during daylight hours in the Connecticut River with a 6.1 m plankton bag seine (2.4 m deep, wing and bag mesh of 0.505 mm) and 30 m lead ropes from 15 May to 20 July 1979–84, 1986, and 1987. No larval sampling was conducted in 1985. One seine haul was taken weekly at 8–12 fixed stations located throughout the major spawning areas (Fig. 1). Further details on sampling and methods of estimating larval abundance from net samples are contained in Crecco et al. (1983).

Juvenile American shad (40–90 mm TL) were collected weekly from 20 July through 15 October 1967–87 at 7–14 fixed stations located above and below the Holyoke Dam (Fig. 1) based on weekly and biweekly seine surveys (Scherer 1974; Foote 1976; Marcy 1976; Crecco and Savoy 1984). The annual juvenile index of relative abundance (IND_t) from 1967 to 1987 was the mean juvenile catch per seine haul (± SE) from all stations and collection dates (Table 2).

The Timing of Density-Dependent Mortality

Analysis

One of the primary objectives of this study was to determine the magnitude and timing of density-dependent mortality for American shad. Peterman (1978, 1982) found that density-dependent mortality for some stocks of the anadromous sockeye salmon, *Oncorhynchus nerka*, was confined mainly to the 4–5 yr oceanic postjuvenile phase. Given that the Ameri-

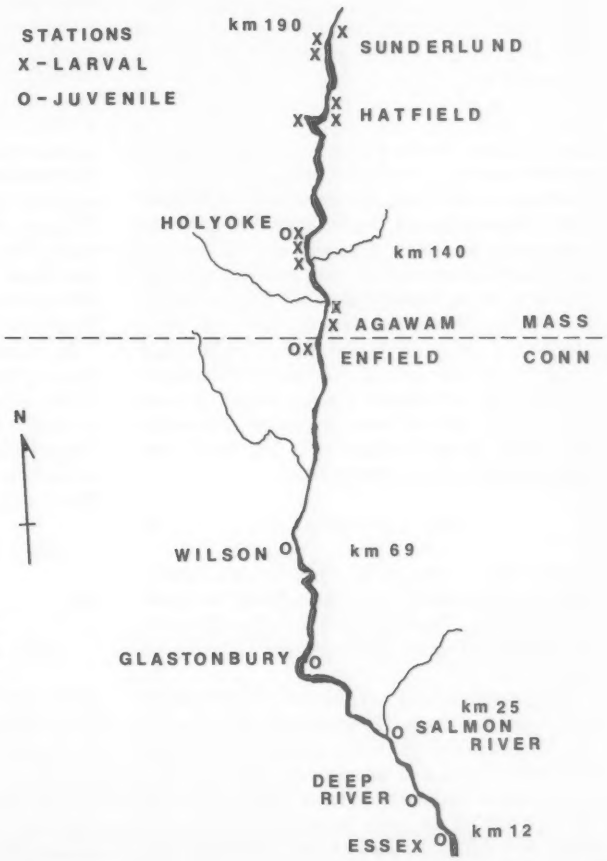

FIGURE 1.—Location of larval and juvenile American shad sampling stations on the Connecticut River.

TABLE 2.—Mean juvenile indices, scaled juvenile abundance from Equation (2) and total egg production for American shad in the Connecticut River from 1967 through 1987. SE = standard errors about the estimates.

Year	Juvenile index	SE	Juvenile abundance $\times 10^3$	SE $\times 10^3$	Total egg production $\times 10^8$	SE $\times 10^8$
1967	20.2	9.4	71,070	33,072	334	70
1968	11.1	1.7	39,053	5,981	404	76
1969	19.0	3.8	68,848	13,770	768	140
1970	27.8	8.2	97,809	28,850	826	190
1971	65.7	14.1	231,151	49,608	848	222
1972	15.3	2.9	53,830	10,203	334	80
1973	12.7	3.4	44,682	11,962	222	60
1974	21.4	6.3	75,292	22,165	612	124
1975	23.7	5.7	83,384	20,054	494	130
1976	22.4	5.9	78,810	20,760	870	160
1977	- - NOT AVAILABLE - -				414	78
1978	27.2	5.9	95,698	20,758	420	108
1979	19.6	3.2	68,959	11,259	496	102
1980	42.7	11.0	150,231	38,701	682	116
1981	16.0	2.7	56,293	9,499	586	100
1982	4.7	1.1	16,536	3,870	1,002	134
1983	26.3	6.6	92,531	23,221	846	154
1984	13.0	2.1	45,738	7,388	1,220	134
1985	17.8	2.7	62,626	9,499	1,110	192
1986	17.0	2.8	59,811	9,851	784	142
1987	44.7	15.1	157,268	53,126	470	74

can shad has a similar 4–6 yr postjuvenile phase as sockeye salmon, we tested Peterman's hypothesis for American shad with key factor analysis (Bellows 1981; Rosenberg and Doyle 1986). We fixed the postjuvenile period for American shad in the Connecticut River between 101 days and 5 years, corresponding to the average age (101 days) at which juvenile shad leave the river (Crecco and Savoy 1985b) and the average age (5 years) when they return to the river as mature adults. The total postjuvenile (age 101 days to 5 years) mortality rates (ZA_t) for the 1967–82 year classes were related to the scaled juvenile indices (J_t) for those year classes (Table 2) in a linear model:

$$ZA_t = a + b(J_t), \quad (1)$$

where $ZA_t = -\log_e(R_t/J_t)$. If significant density-dependent mortality is present during the postjuvenile stage, the slope (b) of Equation (1) would be positive and differ significantly ($P < 0.05$) from zero.

The juvenile indices were scaled to thousands of fish (J_t) so that the y-axis intercept in Equation (1) directly estimates the mean density-independent mortality ($Z_{I\,\mathrm{post}}$), and the slope (b) times the geometric mean juvenile abundance (GM) from 1967 through 1987 is the mean density-dependent mortality rate ($Z_{D\,\mathrm{post}}$). Total juvenile abundance (J_t) was estimated by multiplying the juvenile indices (IND_t) by a scalar (SC):

$$SC = [GR \exp(-EZA) \cdot GM] = 3{,}518.3, \quad (2)$$

where GR is the geometric mean total adult recruitment for 1967 through 1982; GM is the geometric mean juvenile index from 1967 through 1987; EZA (4.85) is the mean total instantaneous mortality among postjuveniles from 1967 through 1982. We estimated EZA as the sum of mortality during the late juvenile period (age 101–365 days), and the subadult stage (age 1–5 years). The mean total instantaneous mortality rate during the late juvenile stage was estimated as 2.65 (0.01 · 265 days), using a mean daily mortality rate of 0.01 (SE = 0.002) extrapolated from the 1979–84 larval and juvenile survivorship curves (Crecco and Savoy 1985b). The mean total instantaneous mortality rate of subadult shad was 2.2, based on an annual instantaneous natural mortality rate of 0.45 from the method of Pauly (1980) plus 0.10 to reflect oceanic fishing mortality (2.2 = 4(0.45 + 0.10)). We estimated the annual natural mortality rate (0.4^F) by substituting the K (0.25, SE = 0.03) and L (55 cm FL, SE = 3 cm) parameters of the von Bertalanffy equation for male and female shad combined and preferred ocean temperature (14°C) of American shad (Leggett and Whitney 1972) into Pauly's multiple regression model. The oceanic fishing mortality estimate (0.10) was based on tagging studies in Delaware Bay (White et al. 1969; Zarbock 1969) and off the New York-New Jersey coast (Nichols 1958).

To determine if density-dependent mortality takes place during the egg and larval stages as Cushing (1980) hypothesized, we related total prejuvenile mortality rates (ZEJ_t) to annual egg production (Eggs_t), and to both egg production (Table 2) and mean June river flow ($J\mathrm{FLOW}$) from 1967 to 1987 (Table 1) in linear regression models:

$$ZEJ_t = a + b(\mathrm{Eggs}_t) \quad (3a)$$

and

$$ZEJ_t = a + b(\mathrm{Eggs}_t) + c(J\mathrm{FLOW}_t), \quad (3b)$$

where $ZEJ_t = -\log_e(J_t/\mathrm{Eggs}_t)$. Mean June river flows (m^3/s) were included in Equation (3b) because previous studies (Crecco and Savoy 1985b, 1987a) have shown that high June flows reduced prejuvenile survival rates, leading to a significant inverse correlation ($r = -0.74$, $P < 0.01$) between the juvenile indices of abundance from 1967 through 1980 and

mean June river flow (Crecco and Savoy 1984, 1985b). Mean June flows (m^3/s) were measured within the major spawning areas (Leggett 1977) by the United States Geological Survey (U.S. Geological Survey 1967–84). We estimated total egg production ($Eggs_t$) in Equations (3a) and (3b) as the product of the mean fecundity of a female American shad times that year's parent stock (PAR_t) of female shad (Table 1). The average fecundity was reduced from 269,000 ova (Leggett 1969) to 200,000 to reflect the average rates of egg retention and incomplete fertilization (Watson 1970; Reed and Russo 1976[7]). Since Leggett (1969) showed that the average fecundity of American shad varied by less than 10% from 1966 through 1973, we were justified in using an average fecundity for all years.

The mean density-independent mortality rate ($Z_{I\,\mathrm{pre}}$) present during the prejuvenile stage was the y-axis intercept (a) in Equation (3b) plus the slope (c) times the overall geometric mean June flow ($GJ\mathrm{FLOW}$) from 1967 through 1987:

$$Z_{I\,\mathrm{pre}} = a + c(GJ\mathrm{FLOW}), \qquad (4)$$

The mean density-dependent mortality rate ($Z_{D\,\mathrm{pre}}$) was the slope (b) of Equations (3a) and (3b) times the geometric mean egg production ($G\mathrm{Egg}$) from 1967 through 1987. A positive and statistically significant slope (b) of prejuvenile mortality on egg abundance would support the Cushing hypothesis that density-dependent mortality takes place before the juvenile stage. If the b estimates of Equations (1), (3a), and (3b) were all positive and significant, our results would support Gulland's (1965) hypothesis that density-dependent mortality occurs over the entire prerecruitment phase.

Results

Although total juvenile abundance varied 14-fold from 1967 through 1982 (Table 2), the total postjuvenile mortality rates (ZA_t) exhibited relatively low variability (95% C.I.: 4.70–5.00) about the estimated mean ($EZA = 4.85$) (Fig. 2). The slope of the linear regression between total postjuvenile mortal-

[7]Reed, R. J., and A. Russo. 1976. American shad research Connecticut River, Massachusetts, 1976. I. Fecundity, egg retention, sex ratio, and age class composition. Unpubl. manuscr., 16 p. Massachusetts Cooperative Fisheries Research Unit, University of Massachusetts, Amherst, MA 01003.

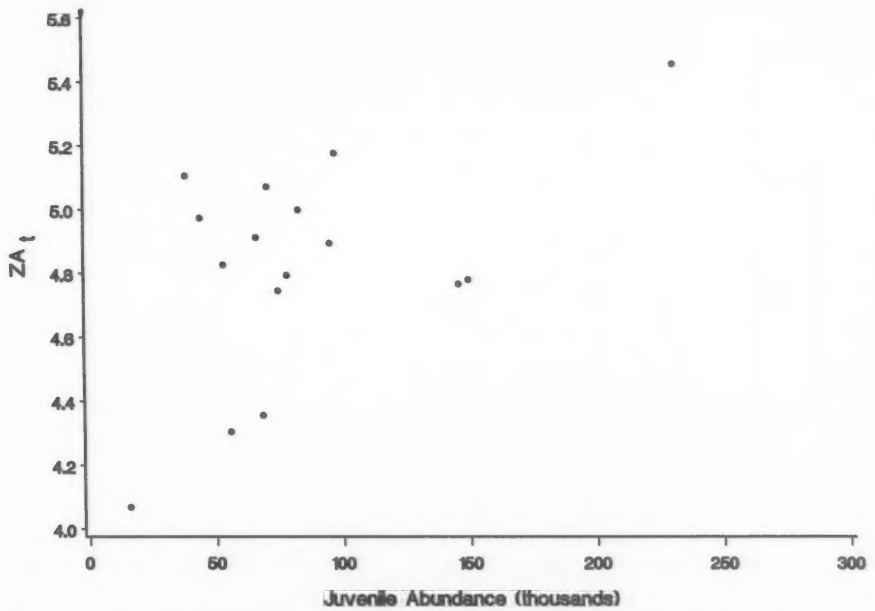

FIGURE 2.—Relationship between American shad postjuvenile mortality (ZA_t) and relative abundance of juveniles (J_t) from 1967 through 1982.

ity rates (ZA_t) and scaled juvenile abundance (J_t) was positive and statistically significant ($P < 0.04$) (Table 3). Since the average density-dependent mortality ($Z_{D\,post} = 0.30$) present during the postjuvenile stage comprised only 6% of the mean total postjuvenile mortality rate ($ZA = 4.85$), density-dependent mortality is not large enough to alter the significant linear correlation ($r = 0.78$, $P < 0.01$) between the juvenile indices (J_t) and adult recruitment (R_t) for the 1967 through 1982 year classes (Fig. 3).

The prejuvenile mortality rates (ZEJ_t) from 1967 through 1987 were positively correlated ($r = 0.70$, $P < 0.0004$) to total egg production ($Eggs_t$) (Fig. 4). Egg production alone explained 49% of the variation in prejuvenile mortality (Table 3) and the slope

TABLE 3.—Estimates of density-dependent (Z_D), density-independent mortality (Z_I) and the fraction of density-dependence ($Z_D/Z_{I+}Z_D$) during the postjuvenile (1967–82) and prejuvenile (1967–87) mortality phases for American shad in the Connecticut River. SE = standard error, and numbers in parentheses = 95% C.I. for Z_D, ZEJ_t = prejuvenile mortality, ZA_t = postjuvenile mortality.

Model	Parameters	SE	Z_D	Z_I	$Z_D/(Z_{I+}Z_D)$
Prejuvenile					
$ZEJ_t = a + b(Eggs_t)$	$a = 5.466$	0.313	1.13	5.47	0.17
	$b = 1.88 \times 10^{-8}$	4.43×10^{-9}	(0.862–1.392)		(0.136–0.203)
	$r^2 = 0.49$				
$ZEJ_t = a + b(Eggs_t)$	$a = 4.287$	0.303	1.18	5.34	0.18
$+ c(J\,Flow_t)$	$b = 1.97 \times 10^{-8}$	2.87×10^{-9}	(1.007–1.351)		(0.158–0.202)
	$c = 0.0028$	0.0005			
	$r^2 = 0.80$				
Postjuvenile					
$ZA_t = a + b(J_t)$	$a = 4.53$	0.15	0.30	4.53	0.062
	$b = 3.49 \times 10^{-6}$	1.51×10^{-6}	(0.035–0.560)		(0.008–0.110)
	$r^2 = 0.275$				

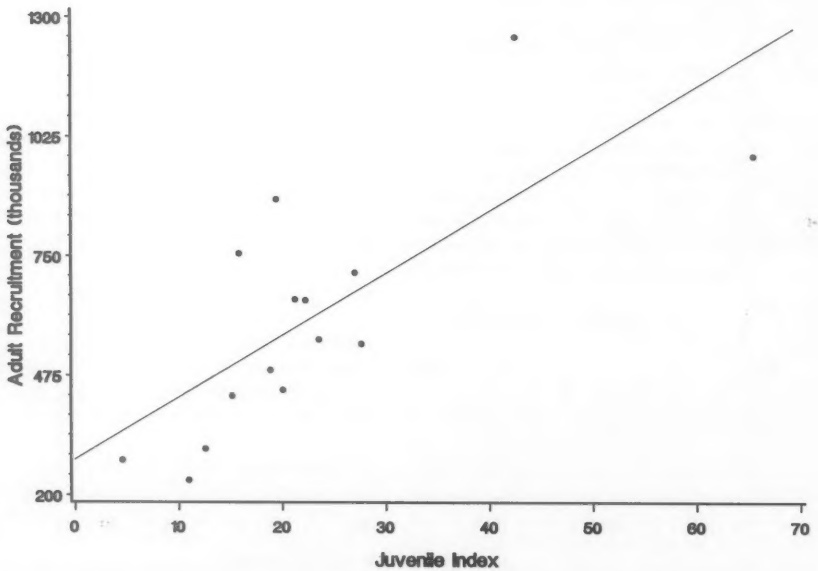

FIGURE 3.—Relationship between total adult recruitment (R_t) and the juvenile abundance indices (IND_t) of American shad from 1967 through 1982.

of the regression differed significantly from zero, indicating the presence of significant density-dependent mortality during the prejuvenile stage. When prejuvenile mortality rates were related to both egg production ($Eggs_t$) and mean June river flow, ($JFLOW_t$), the multiple regression model accounted for 80% of the variability in prejuvenile mortality (Table 3), and the slope estimates for egg production (b) and June flow (c) were positive and highly significant. Note that the standard error (SE) about the slope estimate (b) was reduced by 60% when June flow effects were considered. These results suggest that prejuvenile mortality rates are affected by a combination of density-dependent (egg production) and density-independent (June river flow) factors.

The mean density-dependent mortality rate during the prejuvenile phase ($Z_{D\,\mathrm{pre}} = 1.18$) from the multiple regression model was four times greater than the mean $Z_{D\,\mathrm{post}}$ value (0.30) for postjuveniles (Table 3), suggesting that 80% (1.18/1.18 + 0.30) of the total compensatory reserve for American shad occurs before the juvenile stage. Whereas compensatory density-dependent mortality may play a significant role in regulating egg and larval abundance during years of high egg production, it is clear that most of the variability (82%) in egg and larval abundance is ascribed to density-independent factors.

Egg, Larval, and Juvenile Mortality, 1979–87

Analysis

To examine how larval and juvenile mortality rates varied with year-class strength, survivorship curves for 19,000–180,000 American shad larvae and 800–3,500 juveniles were developed annually from 1979 to 1987 following the techniques of Lough (1976) and Hewitt et al. (1985). Mortality rates could not be estimated directly for prolarvae because American shad yolk-sac larvae (7–9 mm TL) remain in deep water (Marcy 1976) and were only partially susceptible to the plankton seine.

All larvae and juveniles collected annually were separated into four length intervals: 1) 10–13 mm TL, reflecting first-feeding larvae with undeveloped pelvic fins (Wiggins et al. 1984); 2) 14–19 mm TL, associated with the onset of pelvic fin development (Lippson and Moran 1974); 3) 20–28 mm TL, representing larvae approaching metamorphosis, characterized by invagination of the gut (Maxfield 1953);

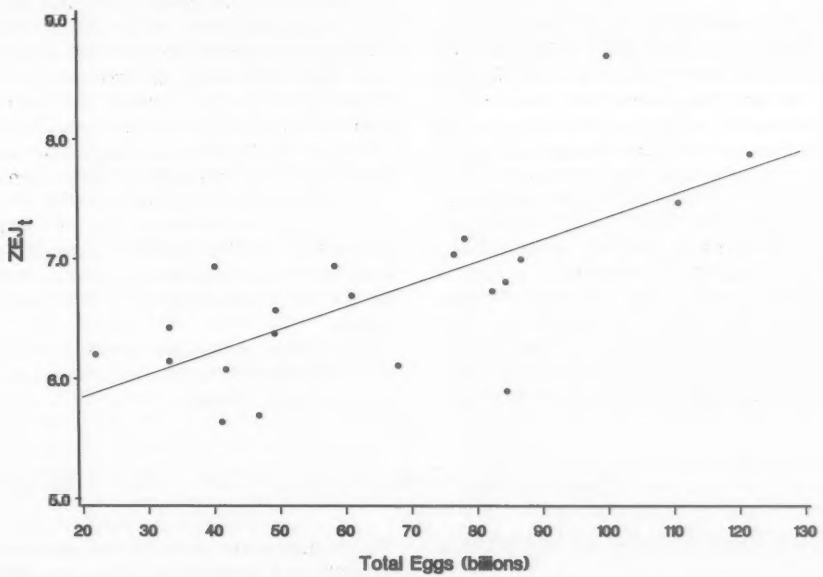

FIGURE 4.—Relationship between American shad prejuvenile mortality (ZEJ_t) and the number of eggs produced ($Eggs_t$) from 1967 through 1987.

and 4) 29–80 mm TL, corresponding to the juvenile stage and the onset of scale development (Marcy 1976). These four groups are hereafter referred to as early larval, midlarval, late larval, and juvenile stages, respectively.

We used otolith increment counts (Savoy and Crecco 1987) to age a subsample of 100–400 American shad larvae and 80–200 juveniles annually from 1979 to 1987. The age-length relationship for larvae and juveniles in all years was well described by the Gompertz growth equation (Crecco et al. 1983; Crecco and Savoy 1985b) so we used a pooled Gompertz equation to describe larval and juvenile growth. The average age (t) of each of the four length groups was estimated by rearranging the Gompertz equation:

$$t = \log_e[K/K - \log_e(L_t(L_0))]/a \quad (5)$$

where L_t = total length (mm); L_0 = length at hatching (8.0 mm); K = growth rate at the inflection point; and a = rate of exponential decay.

The daily instantaneous mortality rates (d) for each stage and their standard errors from 1979 through 1987 were estimated by an exponential model,

$$N_t = \mathrm{A}\ \exp(-dt), \quad (6)$$

that related abundance (N_t) and age (t) by nonlinear regression methods (SAS 1982). The total instantaneous mortality rates of early (ZEL_t), mid (ZML_t), and late (ZLL_t) larvae and juveniles (ZJ_t) were estimated by multiplying the corresponding daily mortality rate (d) by the average duration (Ds = days) within each stage. Previous studies (Crecco and Savoy 1985a; Savoy and Crecco 1987) found that the growth rates of early (10–13 mm) and midlarvae (14–19 mm) were positively correlated with June water temperatures, whereas the growth of late larvae and juveniles were independent of river temperatures. As a result, we adjusted the stage duration (Ds) of early and midlarvae with the mean June temperatures (U.S. Geological Survey 1979–87) from 1979 through 1987 and the larval growth-temperature equations (Crecco and Savoy 1985b: table 7).

We estimated total egg and prolarval mortality rates (ZE_t) indirectly from 1979 through 1987 by subtracting the sum of larval (ZEL_t, ZML_t, ZLL_t), juvenile (ZJ_t) and postjuvenile (ZA_t) mortality rates from the total prerecruitment mortality rate ($Z\mathrm{Total}_t$):

$$ZE_t = Z\mathrm{Total}_t - (ZEL_t + ZML_t + ZLL_t + ZJ_t + ZA_t), \quad (7)$$

where $Z\mathrm{Total}_t = -\log_e(R_t/\mathrm{Eggs}_t)$. However, since the 1983 through 1987 year classes have not been fully recruited to the spawning population, we estimated total adult recruitment (Rp_t) for those year classes by the following environment-dependent stock-recruitment model:

$$Rp_t = 24.29\ (PAR_t)\ \exp(-0.0052 \cdot P_b)\ \exp(-0.0032 \cdot P_a)\ \exp(-0.0025 \cdot J\mathrm{FLOW}_t) \quad (8)$$

Adult recruitment was estimated independently of the juvenile indices by substituting each year's parent stock size (PAR_t), mean June flow (JFLOW), female parent stock lifted over the Holyoke Dam (P_a), and female parent stock below the Holyoke Dam (P_b) (Table 1) into the model. This nonlinear model was shown (Lorda and Crecco 1987) to be a good predictor ($r^2 = 0.81$, $P < 0.001$) of adult recruitment (R_t) for the 1966 through 1982 year classes. Moreover, the predicted recruitment levels (R_t) of the 1983 through 1987 year classes from Equation (8) were closely correlated ($r = 0.92$, $P < 0.01$) with the corresponding juvenile abundance (J_t) for those years (Table 4) which is consistent with the positive correlation ($r = 0.78$, $P < 0.01$) between adult recruitment and the 1967–82 juvenile indices (Fig. 2). This justifies the use of Equation (8) to predict adult recruitment, total mortality, and postjuvenile mortality rates for the 1983–87 year classes.

The standard errors about the egg mortality rates (ZE_t) were derived as the sum of the variances of all other terms (Cochran 1965):

$$\mathrm{SE}_{ZE}^2 = \sqrt{\mathrm{SE}_{ZEL}^2 + \mathrm{SE}_{ZML}^2 + \mathrm{SE}_{ZLL}^2 + \mathrm{ZJ}^2 + \mathrm{SE}_{ZA}^2 + \mathrm{SE}_{Z\mathrm{Total}}^2} \quad (9)$$

The standard errors about the total prerecruitment ($Z\mathrm{Total}_t$) and postjuvenile (ZA_t) mortality rates (Table 5) were based on the same principle as Equation (9) (App. 1).

TABLE 4.—Predicted total adult recruitment of American shad from the environmental dependent stock-recruitment model (Equation (8)), 95% confidence limits about the recruitment values and juvenile abundance for the 1983–87 year classes.

Year	Predicted adult recruitment $\times 10^3$	95% C.I.	Juvenile abundance $\times 10^3$
1983	634	362–906	92,531
1984	196	112–280	45,738
1985	555	317–793	62,626
1986	587	335–839	59,811
1987	955	547–1,363	157,268

TABLE 5.—Estimates of the total ($ZTotal_t$) and postjuvenile (ZA_t) instantaneous mortality rates and their standard errors (SE) for American shad from 1979 through 1987.

Year	$ZTotal_t$	SE	ZA_t	SE
1979	10.94	0.26	4.36	0.23
1980	10.90	0.24	4.78	0.32
1981	11.26	0.25	4.31	0.25
1982	13.00	0.27	4.77	0.34
1983	11.80	0.30	4.98	0.36
1984	13.34	0.26	5.45	0.28
1985	12.21	0.29	4.72	0.28
1986	11.80	0.30	4.62	0.29
1987	10.80	0.28	5.10	0.47

Given that ZE represents total mortality throughout the egg and prolarval period, daily egg mortality rates were determined by dividing ZE by the average duration (Ds) of the egg and prolarval stages of American shad in the Connecticut River. Watson (1968) reported an inverse relationship between the incubation period (D) of shad eggs and water temperature (T) by the expression:

$$D = 120.95 \exp(-0.154 \cdot T). \quad (10)$$

To determine the duration (Ds) of the egg stage from 1979 through 1987 we substituted the mean June temperatures for the Connecticut River (U.S.G.S. Annual Water Year Reports 1979–87) into Equation (10).

The total number of prolarvae (age 2 days) and early larvae (age 10 days) for the 1979 through 1987 year classes was estimated by

$$NE_t = \text{Eggs}_t \cdot \exp(-ZE_t) \quad (11)$$

and

$$NF_t = \text{Eggs}_t \cdot \exp(-ZE_t - ZEL_t) \quad (12)$$

respectively, where NE_t is the estimated number of prolarvae larvae and NF_t is the number of early larvae. The abundance of older larvae and juveniles from each year class was estimated by adding their respective total mortality rates to Equation (12). To determine the life stage(s) at which year-class strength is established, we related the stage-specific total mortality rates and abundance estimates to the number of adult recruits (R_t or Rp_t) from the 1979–87 year classes in several linear models. If year-class strength is established early, there should be a significant positive correlation between the number of prolarvae (NE) and early larvae (NF) and adult recruitment, and total mortality rates during these early stages (ZE and ZEL) should be inversely related to adult recruitment.

To determine the extent of density-independent mortality at the egg, larval, and juvenile stages, we correlated the stage-specific total mortality rates from 1979 through 1987 to mean May and June river flows (m^3/s) and water temperatures (°C) in several linear models. May and June hydrographic and meteorological parameters were used because they coincide with egg, larval, and juvenile development in the Connecticut River (Leggett 1977) and were the only monthly abiotic variables that were significantly linked to adult shad recruitment from 1966 to 1980 (Crecco and Savoy 1984, 1987c). May and June water flows and temperatures were recorded by the U.S. Geological survey (U.S. Geological Survey 1966–1980) within the major spawning areas (river km 89) of American shad (Leggett 1977).

Results

The mean daily mortality rates from 1979 through 1987 declined by an order of magnitude from the egg through the juvenile stages (Table 6). Total egg mortality rates were relatively high (mean ZE = 2.584, cv = 18.5%) and were inversely correlated ($r = -0.76$, $P < 0.03$) with adult recruitment (R_t or Rp_t) from those year classes (Table 7). These data indicate that shad eggs and prolarvae (age 1–2 days) from 1979 through 1987 experienced high (85–96%) mortality that was directly linked to year-class success.

The total mortality rates (ZEL) among early larvae were slightly lower and more variable (mean ZEL = 1.608, cv = 31.5%) than the egg mortality rates (Table 6), and were also inversely related ($r = -0.83$, $P < 0.01$) to adult recruitment from 1979 through 1987. By contrast, the total mortality rates of older larvae (ZML and ZLL) and juveniles (ZJ)

TABLE 6.—Stage-specific total instantaneous mortality rates of egg, larval, and juvenile American shad from 1979 to 1987. SE = stage-specific standard errors; cv = coefficient of variation, Days = duration of each stage.

Year or statistic	Instantaneous total mortality									
	Egg + pro-larvae (day 2)		Early larvae (day 3–9)		Mid-larvae (day 10–18)		Late larvae (day 19–29)		Juvenile (day 30–100)	
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
1979	2.481	0.554	1.323	0.245	1.116	0.189	0.330	0.110	1.330	0.280
1980	1.853	0.819	1.218	0.186	1.096	0.336	0.693	0.099	1.260	0.280
1981	2.580	0.684	1.836	0.108	0.408	0.328	0.726	0.154	1.400	0.210
1982	2.940	0.501	2.144	0.152	1.160	0.210	0.726	0.187	1.260	0.210
1983	3.012	0.785	1.400	0.546	0.522	0.234	0.836	0.143	1.050	0.140
1984	2.706	0.601	2.520	0.352	0.640	0.330	0.484	0.242	1.540	0.280
1985	---------- NO DATA ----------								1.330	0.280
1986	3.158	0.652	1.323	0.196	1.206	0.261	0.374	0.066	1.120	0.280
1987	1.944	0.852	1.098	0.180	0.864	0.128	0.464	0.088	1.330	0.210
Z	2.584		1.608		0.877		0.579		1.286	
SE	0.169		0.179		0.111		0.066		0.051	
cv	0.185		0.315		0.359		0.325		0.120	
Days	7.2		6.9		8.9		11.0		70.0	
Daily *Z*	0.359		0.233		0.099		0.053		0.018	

TABLE 7.—Correlations between stage-specific total mortalities and adult recruitment and several abiotic factors from 1979 to 1987 for American shad. *P* = probability levels.

Stage	Adult recruitment	May flow	May temperature	June flow	June temperature
Egg	−0.76	0.38	−0.08	0.66	−0.59
P	0.03	0.35	0.85	0.08	0.13
Early	−0.83	0.42	−0.21	0.81	−0.64
P	0.01	0.29	0.62	0.01	0.09
Mid	0.16	−0.41	0.49	0.09	−0.34
P	0.71	0.32	0.22	0.83	0.42
Late	−0.02	0.20	−0.51	−0.13	0.18
P	0.96	0.64	0.20	0.75	0.68
Juv	−0.19	0.05	0.02	0.26	−0.08
P	0.65	0.91	0.97	0.53	0.86

were highly variable, but showed no relationship to adult recruitment.

Given that high (94–99%) egg and early larval mortality rates were inversely related to year-class strength, the abundance of first-feeding larvae (age 10 days) was closely correlated ($r = 0.84$, $P < 0.01$) with adult recruitment (Rp_t) from 1979 through 1987 (Table 8). Because year-class strength from 1967 through 1987 was independent ($r = -0.15$, $P < 0.46$) of egg production ($Eggs_t$), our results suggest that year-class strength of American shad is determined by the number of shad that survive the embryonic and early larval stages.

Early larval mortality rates from 1979 to 1987 were positively correlated with mean June river flows. No such relationships were evident for any other stage-specific mortalities (Table 7). The high egg and early larval mortality rates (Table 6) and relative failure of the 1982 and 1984 year classes coincided with major storm events in mid-June 1982 and late May 1984 (Crecco and Savoy 1984) which increased river flows and kept water temperatures below 17°C until late June. The high river flows in 1982 and 1984 were also coupled with the highest parent stocks on record since 1967 (Table 1). By contrast, the relatively low egg and early larval mortality rates for the dominant 1980 and 1987 year classes were associated with low June river flows, a steady rise in June water temperatures (Crecco and Savoy 1984) and low to moderate size parent stocks (Table 1). These results suggest that dominant year classes of American shad are most likely to occur when lower than normal June flows are coupled with relatively small spawning stocks.

Prejuvenile Density-Dependent Mortality: A Closer Look

Analysis

Having estimated that 82% of the density-dependent mortality for American shad takes place before the juvenile stage (Table 3), we attempted to estimate the relative contribution of density-dependent mortality during the egg, early, mid-, and late larval and juvenile stages from 1979 through 1987. We related egg mortality rates (ZE_t) from

TABLE 8.—Relationship between the number ($\times 10^6$) of American shad at each life history stage and adult recruitment from each year class. r = correlation coefficient and P = probability levels from 1979 to 1987.

	Stage						
Year-class	Egg	Pro-larvae	Early larvae	Mid-larvae	Late larvae	Juvenile	Adult[1]
1979	496	41.5	11.0	3.6	2.6	0.7	882
1980	682	106.9	31.6	10.6	5.3	1.5	1,256
1981	586	44.4	7.1	4.7	2.3	0.6	758
1982	1,002	53.0	6.2	1.9	0.9	0.3	282
1983	846	41.6	10.3	6.1	2.6	0.9	634
1984	1,220	81.5	6.6	3.5	2.1	0.5	196
1985	1,110	----------	----------	NO DATA	----------	----------	555
1986	784	33.3	8.9	2.7	1.8	0.6	587
1987	470	67.3	22.4	9.5	5.9	1.6	955
r =	−0.15[2]	0.33	0.84	0.80	0.79	0.82	
P =	0.46	0.43	0.01	0.02	0.02	0.01	

[1]Predicted or observed recruitment in thousands.
[2]Correlation coefficient for egg abundance and recruitment was based on the 1967–87 data (Tables 1, 2).

1979 to 1987 to total egg production (Eggs_t) in a linear model:

$$ZE_t = a + b(\text{Eggs}_t). \quad (13)$$

As before, significant density-dependence would be shown if the slope (b) in Equation (13) was positive and differed significantly from zero.

The cumulative amount of density-dependent mortality during the egg and early larval stages combined was estimated by summing the instantaneous total mortality rates of early larvae (ZEL_t) and eggs (ZE_t) and then regressing the total ($ZE_t + ZEL_t$) against egg production as in Equation (13). This procedure was repeated for each subsequent stage by adding their respective instantaneous total mortality rates. We then estimated the relative magnitude of density-dependent mortality (Z_D) at each stage by multiplying the slope (b) of each regression equation by the geometric mean egg production ($G\text{Egg}$) from 1967 through 1987. The density-independent mortality rate (Z_I) at each stage was expressed by the y-axis intercept (a) of each regression equation. The percentage contribution of density-dependent mortality ($\%Z_D$) for each period was the ratio of Z_D to total mortality ($Z_D + Z_I$) times 100.

Results

Our results showed that significant density-dependent mortality first occurs during the early larval stage and persists for all stages thereafter (Table 9). The percentage contribution of density-dependent mortality ($\%Z_D$) rose from 24% of the total during the egg stage to 41% during the early larval stage, and then declined during the mid- and late larval stages as the magnitude of density-independent mortality increased. The mean density-dependent mortality rate for the egg and early larval

TABLE 9.—Relationship between the cumulative mortality rates and parent stock sizes (Eggs_t). The cumulative mortality rate was egg mortality (ZE) plus early larval mortality ($Z2$), midlarval mortality ($Z3$), late larval mortality ($Z4$), and juvenile mortality ($Z5$). Z_D = density-dependent mortality rate, Z_I = density-independent mortality rate, $\%Z_D$ = percentage density-dependent mortality, $\%Z_I$ = percentage density-independent mortality, t = student t-statistic.

Model	b parameter	SE(b)	t	Z_D	Z_I	$\%Z_D$	$\%Z_I$
$ZE = a + b(\text{Eggs}_t)$	9.89×10^{-9}	6.40×10^{-9}	1.55	0.59	1.83	24	76
$Z2 = a + b(\text{Eggs}_t)$	2.57×10^{-8}	7.76×10^{-9}	[1]3.31	1.54	2.24	41	59
$Z3 = a + b(\text{Eggs}_t)$	2.44×10^{-8}	8.16×10^{-9}	[1]2.99	1.46	3.21	31	69
$Z4 = a + b(\text{Eggs}_t)$	2.60×10^{-8}	7.74×10^{-9}	[1]3.36	1.55	3.67	30	70
$Z5 = a + b(\text{Eggs}_t)$	2.69×10^{-8}	7.50×10^{-9}	[1]3.59	1.61	4.88	25	75

[1]Significant student t-statistic at the $P < 0.01$ level and SE(b) = standard error of b.

stages combined (Z_D = 1.54) between 1979 and 1987 was not significantly different (Table 9) from the total density-dependent mortality rate ($Z_{D\,pre}$ = 1.18) estimated during the prejuvenile period from 1967 to 1982 (Table 3), suggesting that nearly all of the density-dependent mortality for prejuvenile American shad occurs before the midlarval stage.

DISCUSSION

Although American shad eggs and early larvae experience high mortality (15–40%/day) in the Connecticut River, the average density-dependent mortality rate ($Z_{D\,pre}$ = 1.18) during those stages comprised a relatively small percentage (18%) of the total prerecruitment mortality. This suggests that most of the annual variability in American shad recruitment is explained by density-independent factors, which is consistent with the significant positive correlation between mean June flow and egg and early larval mortality rates, and with the significant inverse correlation ($r = -0.74, P < 0.001$) between mean June river flow and adult recruitment from the 1967 through 1982 year classes (Crecco and Savoy 1984, 1987b). Whereas these data illustrate that density-dependent mortality plays a minor role in governing annual variability in American shad recruitment, this does not mean that compensatory processes are trivial. As pointed out by Ricker (1954) and others (Cushing 1974; Garrod and Horwood 1984), only a small amount of density-dependent mortality is required to stabilize the growth potential of fish populations because density-dependent effects become progressively more effective at higher egg and larval densities (Shepherd and Cushing 1980; Murray 1982).

Although our results on American shad support the Gulland (1965) hypothesis that density-dependent mortality persists throughout the prerecruitment period, most (82%) of the density-dependent mortality occurs during the egg and early larval stages. Our average estimate of density-dependent mortality (Z_D = 1.54) during the early larval periods does not differ significantly from the mean Z_D value (1.34) estimated among the 5-d larval cohorts in 1983 and 1984 (Crecco and Savoy 1987a), or from the mean density-dependent mortality rate Z_D (1.21) estimated by stock-recruitment methods for the entire prerecruitment period (Lorda and Crecco 1987). That year-class strength is established early in the ontogeny of American shad is supported further by the significant positive correlation (r = 0.84, $P < 0.009$) between the relative abundance of early larvae and all subsequent stages from 1979 through 1987 and adult recruitment from those year classes (Table 8).

The main causes of density-dependent mortality are thought to be predation, competition, and cannibalism (Ricker 1954). Since adult American shad are not thought to feed in freshwater (Walburg and Nichols 1967), we can probably eliminate cannibalism as a mechanism for significant density-dependent mortality during the egg and early larval stages. Therefore, density-dependent mortality among early American shad larvae is most likely caused by intraspecific competition for food or space and predation. The exact underlying density-dependent mortality mechanisms are difficult to quantify because the outcome of competition and predation may depend on June flow effects shown here (Table 3) and elsewhere (Crecco and Savoy 1987a, b) to be the principal density-independent factor. High June river flows have been shown to reduce June river temperatures (Crecco and Savoy 1984) and the growth rates of shad eggs (Watson 1968) and early larvae (Crecco and Savoy 1985b). Because slower growing larvae may be susceptible to predation for a longer period of time (Hunter 1976), periods of high flow may indirectly enhance egg and larval predation. Additionally, since high flows reduce the spatial patchiness (Crecco and Savoy 1987a), abundance and availability of river zooplankton (Whitton 1980; Threlkeld 1986), high flows may result in increased levels of competition among American shad larvae for available prey, especially if shad larvae are capable of depleting local aggregations of edible zooplankton. Periods of high runoff that coincide with peak larval production, such as in June 1982 and 1984, may advect larvae and their zooplankton prey from eddies and backwaters where they are normally found (Cave 1978) to areas of high predator abundance. In light of the many ways in which June flows potentially mediate larval mortality, it is unlikely that a single compensatory mechanism is responsible for the relatively high density-dependent mortality rate ($Z_{D\,pre}$) among early larvae.

Since egg and prolarval shad have endogenous food reserves, density-dependent mortality of these stages is likely due to predation and competition for sites among spawning adults. As spawning stocks reach high densities, such as in 1982–84, crowding of adult fish on the spawning grounds may result in a reduction in the number of eggs released (Goodyear 1980). In addition, since the amount of spawning habitat in the Connecticut River can be considered fixed from year to year, larger spawning stocks are more apt to deposit an increasing percentage of eggs in unfavorable areas. Layzer (1974)

noted that the highest survival rates of American shad eggs occurred over gravel and rubble substrates. Since these areas generally have higher water velocities, eggs lodged within the interstices of the gravel and rubble are less likely to be eaten by predators or covered by silt. Dense aggregations of eggs may also be highly susceptible to fungal agents (Leach 1925), which could then act as efficient density-dependent predators. However, since predators of American shad eggs and larvae in the Connecticut River have not yet been identified, density-dependent losses are difficult to quantify. Also, predation mortalities in general may be either density-dependent or density-independent, depending on the functional response between the predator and the prey (Hassell 1978), and whether predators actively search for discrete aggregations of eggs and larvae or prey on randomly encountered eggs and larvae (Gulland 1987).

In the absence of direct egg mortality estimates of American shad, the accuracy of our egg mortality estimates (ZE_t) from Equation (7) are difficult to evaluate, particularly since the standard errors about the estimates are highly variable (Table 6). To provide an independent estimate of daily egg mortality, we used the multiple regression method of McGurk (1987) to estimate the average daily egg mortality rate. This method requires an estimate of the patchiness and the mean dry weight of a shad egg. We derived Lloyd's patchiness index ($\bar{x}$ = 7.26, SE = 0.376) for American shad eggs in the Connecticut River from the 1974–75 egg surveys in the Holyoke Dam impoundment (NUSCo 1977). Substituting the mean weight of a shad egg (0.00025 g, Leggett 1969) and the mean patchiness index into McGurk's equation 4, yields an instantaneous daily egg mortality rate of 0.34 which closely approximates our average estimate (0.36) from 1979 to 1987 (Table 6).

Lastly, since it is presently unknown if younger (smaller) virgin female American shad produce smaller, less viable eggs than older shad as was reported for cod, *Gadus morhua*, (Knutsen and Tilseth 1985), the contribution of the age structure to the parent progeny relationship (Rosenberg and Doyle 1986) should be considered. This issue and an examination of whether egg deposition rates are density-dependent should be addressed by monitoring egg retention rates among postspawning American shad.

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APPENDIX 1

The total prerecruitment ($Z\text{Total}_t$) and postjuvenile (ZA_t) mortality rates from 1979 through 1987 were estimated by

$$Z\text{Total}_t = -\log_e(Par_t * 200{,}000) - \log_e(R_t)$$

and

$$ZA_t = \log_e(J_t) - \log_e(R_t),$$

respectively. The standard errors about $Z\text{Total}_t$ and ZA_t were estimated as the sum of the variances (Cochran 1965):

$$\text{SE}_{Z\text{Total}_t} = \sqrt{\frac{S^2_{R_t}}{n_t} + \frac{S^2_{Par_t}}{n_t}}$$

and

$$\text{SE}_{ZA_t} = \sqrt{\frac{S^2_{J_t}}{n_{J_t}} + \frac{S^2_{R_t}}{n_t}}$$

respectively. The variance estimates ($S^2_{R_t}$, $S^2_{Par_t}$) of adult recruitment and spawning stock size were calculated from the log transformed estimates from the daily lift rates at the Holyoke Dam, where n_t is the total number of days in which 99% of the American shad were lifted. The variance ($S^2_{J_t}$) about the juvenile abundance estimates (J_t) was based on the log transformed catches per seine haul from all stations and collection dates, where n_{J_t} is the total number of seine hauls made in that year.

METABOLIC RESPONSES OF SPOT, *LEIOSTOMUS XANTHURUS*, AND ATLANTIC CROAKER, *MICROPOGONIAS UNDULATUS*, LARVAE TO COLD TEMPERATURES ENCOUNTERED FOLLOWING RECRUITMENT TO ESTUARIES

DONALD E. HOSS, LINDA COSTON-CLEMENTS, DAVID S. PETERS, AND PATRICIA A. TESTER[1]

ABSTRACT

The larvae of marine fishes that spawn during fall-winter in coastal North Carolina waters experience a decrease in temperature as they enter estuarine nursery areas. To determine the effect of changes in temperature on larval metabolism, the oxygen consumption of spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, was measured and their QO_2 and Q_{10} values were determined. Atlantic croaker respiration decreased with temperature at rates that would be expected if no compensation or stress were involved. Spot showed unexpectedly high respiration rates at low temperature. The increased respiration is apparently due to stress. Based on laboratory feeding and growth data, we concluded that spot are subject to an energy deficit at ≤10°C. We infer the timing of larval immigration corresponds with environmental temperatures reaching tolerable levels. Atlantic croaker larvae immigrate earlier in the winter and are exposed to cold water for longer periods than spot larvae. Our conclusion is that stress and energy loss experienced by early immigrating spot larvae may result in increased mortality.

The larvae of fishes that spawn during fall and winter in offshore North Carolina waters experience a decrease in both temperature and salinity as they enter estuarine nursery areas (Fig. 1). The spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, two sympatric species of Sciaenidae, are representative of winter spawning species off the North Carolina coast.

Previously, we have examined the effects of increased temperature on the oxygen and food consumption of the postlarval stages of these two species (Hoss et al. 1971, 1974; Peters and Kjelson 1975). In this paper we continue our research on the early life history of these species and evaluate how decreasing water temperature, encountered following recruitment into estuarine waters, might affect oxygen consumption, food consumption, and ultimately survival.

Crawshaw et al. (1981) stated that young fish typically select warm shallow water because 1) it permits more rapid growth owing to higher metabolism, given an adequate food supply, and 2) the predation by larger fish is less in shallow water. For some fish this explanation is plausible, but this does not apply to the larvae of many winter-spawning marine fishes which begin life in relatively warm coastal waters and then enter colder estuarine waters. For these species we expect that metabolism and growth of the estuarine immigrants should be reduced (Brett 1956). The specific objective of this paper is to describe how decreasing temperature affects the metabolism of larval fish as they are moved from warm to cold water by a combination of passive and active transport mechanisms that are not, as yet, completely understood. Oxygen consumption is a common method of estimating metabolic activity, which frequently changes in response to environmental conditions (O'Hara 1968). In this study we measured routine oxygen consumption which is the amount used by fish whose only movements are spontaneous.

STUDY AREA AND METHODS

Spot and Atlantic croaker spawn off the North Carolina coast inshore of the Gulf Stream over the continental shelf (Hildebrand and Cable 1930; Dawson 1958; Powles and Stender 1978). Here, spot spawn from October to February, but principally from December to January while Atlantic croaker spawn from September to May but principally between October and December (Lewis and Judy 1983). After between 30 and 60 days in coastal

[1]Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

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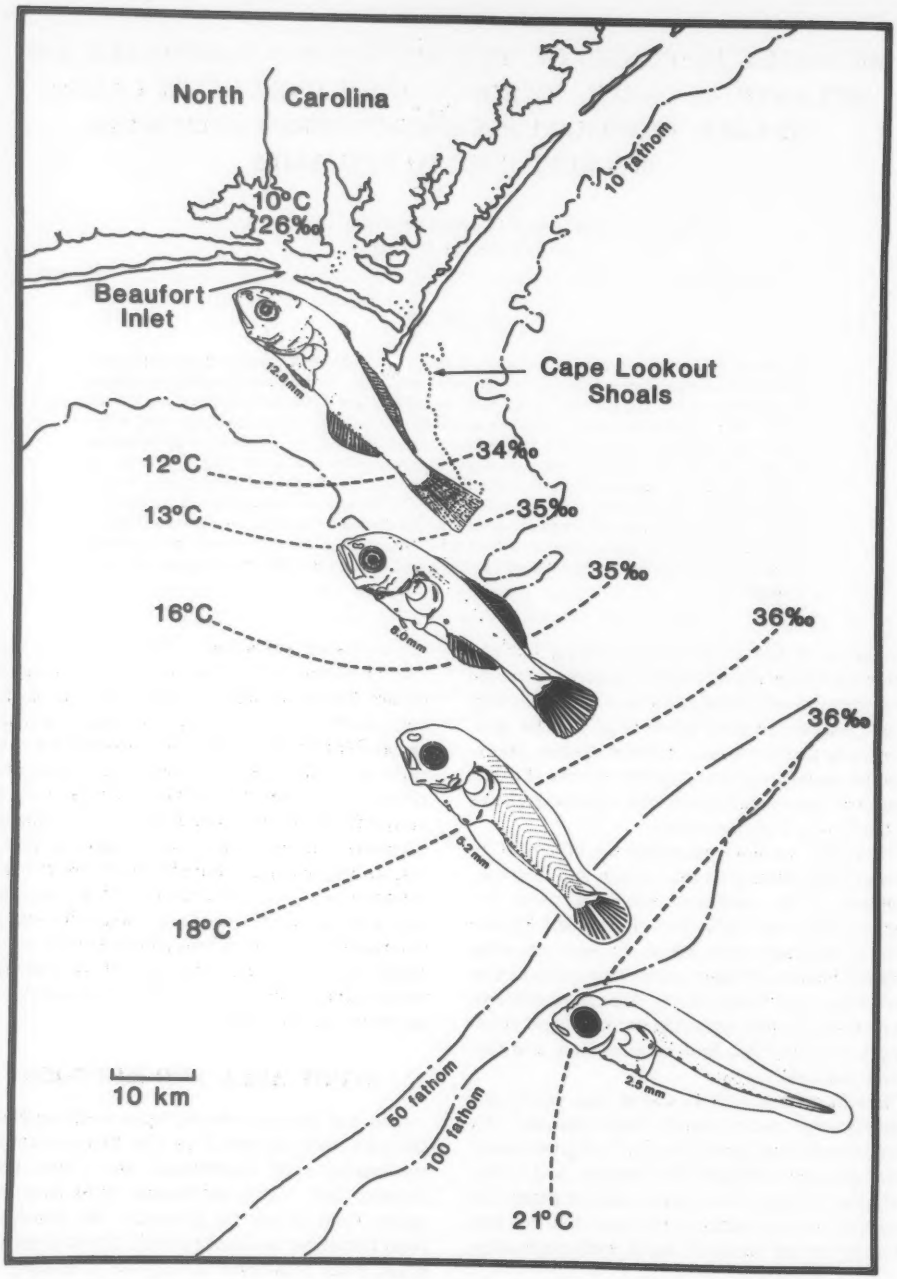
North Carolina
10°C
26‰
Beaufort Inlet
10 fathom
Cape Lookout Shoals
12.8 mm
34‰
12°C
13°C
35‰
35‰
16°C
8.0 mm
36‰
36‰
6.2 mm
18°C
10 km
50 fathom
100 fathom
2.5 mm
21°C

waters (Warlen 1982; Warlen and Chester 1985), the larvae enter estuaries where they develop into juveniles. In the spawning area, water temperatures are usually between 18° and 25°C (Fahay 1975; Hettler and Powell 1981). The fish encounter decreasing temperatures as they move inshore to the estuarine nursery areas. In the lower Newport River estuary, for example, mean water temperatures between November and March may range from 14° to 6°C with the highest temperatures during this period occurring in November and the lowest in January (Hoss 1974).

Larvae of Atlantic croaker and spot were obtained from both field collections and eggs spawned in the laboratory. Older larvae were captured in a bridge net (Hettler 1979) and held in the laboratory for no more than a week prior to use. First feeding larvae were obtained from spawned fish, reproduced by the methods of Hettler and Powell (1981), and then were reared at experimental temperatures.

Oxygen consumption was measured with a differential respirometer (Umbreit et al. 1964), following procedures used by Hoss, Hettler, and Coston (1974). Fish were transferred to 15 mL respiration flasks and, following a 2-h acclimation period, their oxygen consumption was measured. Numbers of larvae per flask varied between 1 and 30, depending on the size of the larvae. Acclimation temperatures were 10°, 15°, and 20°C. Notochord or standard lengths and dry weights were obtained for individual fish.

The metabolic equation $Q = aW^k$, was used to describe the relation between oxygen consumption and dry weight of fish acclimated at 10°, 15°, and 20°C. In this equation, W is the weight of the fish, and a and k are constants for the species obtained from least-squares regression of the log of oxygen consumption on the log of weight (Winberg 1956). A k value of 0.67 implies that oxygen consumption varies in proportion to surface area, whereas a value of 1 indicates that respiration varies in proportion to weight.

We used the metabolic equation to estimate oxygen consumption of larvae of equal weight at different temperatures. We compared larvae of 4 mg dry weight because this is the realistic estimate of their weight as they are transported from coastal to estuarine waters (Warlen 1982; Warlen and Chester 1985).

Growth and feeding rates of small spot (≃20 mm SL) collected from the Newport River were calculated from data collected in the laboratory at several temperatures. Wet weights (≃15–30 mg) were recorded to the nearest milligram, and 10 fish were randomly assigned to 4 L test and control containers. Control fish were dried to determine the dry/wet weight ratio, which was then used to estimate initial dry weight of experimental fish. One experiment was conducted at 6°, 8°, 10°, 12°, and 16°C, and two experiments were conducted at 18°C. In all cases fish were fed newly hatched brine shrimp several times a day to assure an ad libitum food supply. After 4–6 days all food was removed; larvae were allowed time to clear their guts and then were dried and weighed.

Growth and feeding rates were expressed as percent of body weight per day. Growth rate was calculated from the expression:

$$\text{Growth rate} = 100\,[(Wn/Wo)^{1/n} - 1]$$

where Wn = dry weight of all fish in a tank at day n
Wo = estimated original dry weight of fish
n = number of days fed.

Calculation of feeding rates required the assumption of constant growth rates. Using original dry weights and calculated growth rates we determined the total dry weight of fish in each container at the beginning of each day. Dry weights of brine shrimp eaten each day divided by the calculated dry weights of fish gives proportion of body weight ingested. These proportions were then summarized as average daily percent of dry body weight ingested.

In order to compare metabolic parameters, i.e., oxygen consumption, feeding, and growth rates, the following conversion factors were used: 1.0 mg dry wt = 5.0 cal (Thayer et al. 1973; Paffenhöffer 1967); 1.0 mg O_2 = 3.38 cal (Phillipson 1966) and 0.7 mg O_2 = 1 mL O_2 at STP. One tenth calorie per fish per day was added to all the rates so that measured zeros could be shown on a log scale.

RESULTS AND DISCUSSION

The regression equations relating oxygen consumption to weight at several temperatures are shown in Table 1. Higher coefficient of determination (R^2) values were found at higher temperatures, a trend best explained by differences in the size range of fish measured at different temperatures. Values for k, were generally comparable to values reported by other investigators for fish of a similar size and at comparable temperatures—Hoss (1974), pinfish; Houde and Schekter (1983), bay anchovy, sea bream, and lined sole; Almatar (1984), herring; and Laurence (1978), cod and haddock.

TABLE 1.—Metabolic equations relating oxygen consumption to body size. $Q = aW^k$ where Q = oxygen consumption ($\mu L\ O_2 \cdot h^{-1}$), a and k are regression coefficients, W is dry wt in mg, N is the number of observations, T the temperature, and R_2 the coefficient of determination.

Species	T	N	W	a	k	R^2
Atlantic croaker	10	52	1.50 – 6.43	1.80	0.66	0.42
	15	65	1.90 –11.71	2.00	1.02	0.65
	20	81	0.013– 9.31	3.59	0.86	0.94
Spot	10	37	1.82 – 8.01	3.63	0.70	0.54
	15	48	2.18 –10.27	3.15	0.64	0.63
	20	79	0.014– 8.91	4.07	0.92	0.97

Comparing between measured oxygen consumption rates at 10° and 15°C and those predicted from Van't Hoff's equation (Vernberg and Vernberg 1972), we conclude that Atlantic croaker show no sign of regulating their oxygen consumption as water temperature is decreased. The difference between oxygen consumption rates based on Q_{10} values of 2 and 3 (Fig. 2) is an expected range. For every 10°C change in temperature, the rate of a chemical reaction typically changes by a factor of 2 to 3. A Q_{10} value of appreciably <2 or more than 3, indicates that some process other than a chemical one is involved (e.g., a change in cell membrane permeability). A Q_{10} of one indicates temperature independence (Vernberg and Vernberg 1972). Our conclusion that Atlantic croaker did not display thermal stress is based on the fact that measured respiration rates at reduced temperatures (10° and 15°C) were within the range expected (Fig. 2A).

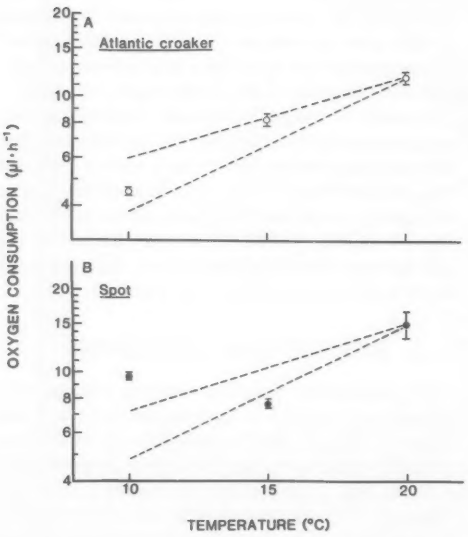

FIGURE 2.—Oxygen consumption rates for 4 mg Atlantic croaker (A) and spot (B) at three temperatures estimated from equations in Table 1. The bars indicate standard errors from regressions in Table 1. Broken lines are estimates of the rates expected based on Van't Hoff's equation, the rate measured at 20°C, a Q_{10} of 2 (upper line) and a Q_{10} of 3 (lower line).

For spot a decrease in temperature from 20° to 15°C resulted in a decrease in oxygen consumption of approximately the amount expected for a Q_{10} of 3. A further decrease in temperature to 10°C, however, caused an increase in the respiration rate. The changes in oxygen consumption at low temperatures could be interpreted either as adaptive, i.e., maintaining a high metabolic rate even at the lower temperature, or inadaptive, i.e., a metabolic breakdown.

Based on feeding, growth, and survival data, however, we think the increase in respiration by spot at 10°C is a result of cold stress, not adaptation. In Figure 3 we present three measures of metabolic rate, ad libitum feeding rate, maximum growth rate, and routine oxygen consumption for spot, all as a function of temperature. Feeding, growth, and oxygen consumption rates decrease with decreasing temperature and the rates are similar over a limited range of the conditions tested (Fig. 3). The rates of decline in feeding and growth from 18° to 12°C approximates that of oxygen consumption from 20° to 15°C. At lower temperatures stress appears to become important. For example, it was not possible to measure growth at 10°C or below because only a fraction of the larvae survived. At 8° and 10°C some of the larvae did not eat and at 6°C none of them did. This agrees with Dawson (1958) who concluded that the lethal minimum temperature for spot is in the 4.0°–5.0°C range and probably varies with size. The intersection of ad libitum feeding rate and routine oxygen consumption occurs at approximately 10°C (Fig. 3). At this temperature there is just enough energy available for routine metabolism. Below this temperature there is not enough energy available even at the ad libitum feeding rate to maintain the larvae, and spot held at this temperature for any length of time would be unlikely to survive.

We conclude from our data on metabolic responses to temperature that spot and Atlantic croaker larvae differ in their response to cold temperatures which prevail at the time of their recruitment to the estuary and that this difference may have important implications for their survival. Both species spawn in warm waters of the continental shelf where the eggs hatch. As the larvae grow they are

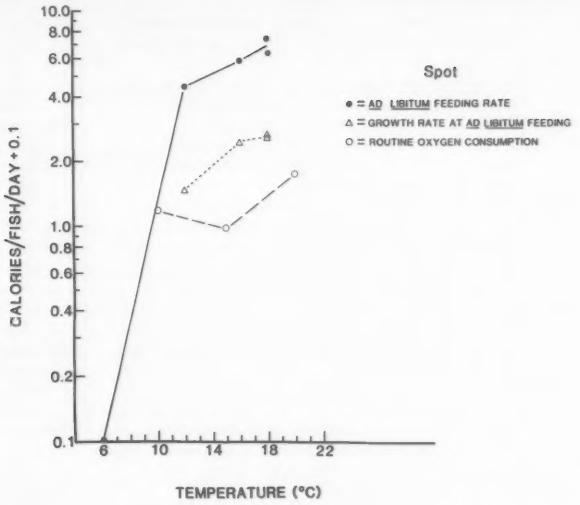

FIGURE 3.—Ad libitum feeding rate, growth rate at ad libitum feeding rate, and routine oxygen consumption for 4 mg dry wt spot at various temperatures between 6° and 20°C.

transported from warm coastal waters into cold estuarine waters. Atlantic croaker are capable of enduring low winter temperatures with decreased metabolic rates that allow for balanced energy intake. Spot, in contrast, show signs of thermal stress manifested as increased respiration rate (at 10°C). This increased metabolism along with no attendant increase in feeding results in an energy deficit and in eventual mortality of the larvae. Species specific differences in the time of entry to the estuary serves as ecological evidence supporting our contention that spot are more susceptible to cold weather. Most spot enter the estuary after the peak in Atlantic croaker immigration and generally after the coldest weather.

Our findings have important implications with respect to recruitment of estuarine-dependent fish which spawn in the ocean during winter. It may be that during severe winters, many of the larvae of cold sensitive species (e.g., spot) that reach the estuary early are killed by cold water temperatures (10°C or less). Thus, only the late arriving larvae survive to recruit into the fishery. The difference in survival between severe and normal winters may help to explain in part the difference between good and poor year classes of certain fish.

Acknowledgments

We thank W. Hettler for providing eggs of laboratory spawned fish, and W. Hettler and J. Govoni for providing critical reviews of the manuscript. This research was funded in part by a cooperative agreement between the National Marine Fisheries Service and the Department of Energy E(49-7)5.

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GROWTH OF PACIFIC SAURY, *COLOLABIS SAIRA*, IN THE NORTHEASTERN AND NORTHWESTERN PACIFIC OCEAN[1]

YOSHIRO WATANABE,[2] JOHN L. BUTLER,[3] AND TSUKASA MORI[4]

ABSTRACT

Growth of the Pacific saury, *Cololabis saira*, from the northeastern and northwestern Pacific Ocean was studied using otolith growth increments. We found that growth of Pacific sauries from the western Pacific was higher than that from the eastern Pacific. Assuming that otolith growth increments are deposited daily, average growth rates from hatching up to 1 year old were 0.62 mm/d in the eastern and 0.85 mm/d in the western Pacific. Because the growth rate changes at around 100 mm, two curves were used to model the growth of Pacific saury in the western Pacific: one for fish up to 100 mm and the other for fish larger than 100 mm. Based on counts of daily increments, Pacific sauries may be short lived. The oldest specimen examined was only 14 months old.

The Pacific saury, *Cololabis saira* (Brevoort), is distributed throughout the North Pacific Ocean and is one of the most important commercial fishes in the northwestern Pacific. The average annual catch of Pacific saury in Japan has been approximately 200,000 t (metric tons) in the last 20 years (Statistics and Information Department, Japan 1985). The catch has varied by an order of magnitude in the last 20 years from a minimum of 63,000 t in 1969 to a maximum of 406,000 t in 1973. Fluctuation in stock size is a major factor in catch variability although economic factors such as fish price may also affect total landings. However, the causes of stock fluctuation in the western Pacific remain unknown. In the eastern Pacific, the Pacific saury has not been exploited but is recognized as a potential fishery resource (Ahlstrom 1968; Smith et al. 1970).

Investigations of the Pacific saury have mainly been devoted to such subjects as systematics, abundance, distribution, migration, and formation of fishing ground in relation to oceanographic conditions (e.g., Hubbs and Wisner 1980; Smith et al. 1970; Odate 1977; Fukushima 1979; Sablin and Pavlychev 1982; Gong 1984). Age determination and growth, however, remain controversial (Hatanaka 1955; Hotta 1960; Novikov 1960; Sunada 1974; Kim and Park 1981), notwithstanding their critical importance for fish stock assessment.

The discovery of daily increments in the otoliths of fishes (Pannella 1971) has made it possible to estimate age and growth of larval and juvenile fishes accurately. Daily increments have been used to age many species of fishes (Jones 1986). Nishimura et al. (1985) reported the presence of growth increments in Pacific saury otoliths observed by scanning electron microscopy and suggested that it is possible to estimate age and growth of Pacific saury by using daily increments in the otolith. The purpose of this paper is to determine the age of Pacific sauries from the eastern and western North Pacific using daily increments and to compare the growth rates in these areas.

MATERIALS AND METHODS

We read otoliths of 75 Pacific sauries from the northeastern and 172 from the northwestern Pacific Ocean. Details of sampling and methods of reading otoliths are summarized in Table 1 and Figure 1. Additional samples from the western Pacific were used to determine the relation between otolith size and fish length. Fish from the eastern Pacific were fixed and preserved in 80% alcohol after capture, and those from the western Pacific were stored frozen and thawed when processed. Because specimens frequently have damaged upper jaws, knob length (the distance from the tip of the lower jaw to the posterior end of the muscular knob at the base of a caudal peduncle) is the standard measure of body size in Pacific saury. All body lengths in this paper are knob length.

[1]Contribution No. 429 from Tohoku Regional Fisheries Research Laboratory.

[2]Tohoku Regional Fisheries Research Laboratory, Fisheries Agency, Shiogama, Miyagi 985, Japan.

[3]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[4]Faculty of Fisheries, Hokkaido University, Hakodate, Hokkaido 041, Japan.

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TABLE 1.—Collection records of saury samples from the eastern (# 1–10) and the western (# 11–22) North Pacific. N = Neuston net; G = Gill net; D = Dip net.

Sample	Date	Location		No.	Size range (KnL mm)	Gear	Micro-scope
		Lat.	Long.				
1	80 06 29	36°02′N	124°04′W	10	19.8–109.0	N	LM
2	80 06 29	36°07′N	123°55′W	10	19.8– 66.0	N	LM
3	80 06 29	36°07′N	123°45′W	10	15.3– 96.0	N	LM
4	81 10 26	46°36′N	127°49′W	5	47.8–235.0	N	LM
5	81 10 27	47°19′N	126°09′W	6	38.0–142.0	N	LM
6	81 10 28	47°20′N	124°30′W	12	23.9–216.0	N	LM
7	81 10 29	46°21′N	127°38′W	1	209.0	N	LM
8	81 10 30	46°38′N	125°54′W	14	20.6– 85.0	N	LM
9	81 11 01	45°21′N	127°38′W	4	27.0– 71.0	N	LM
10	81 11 02	45°38′N	124°51′W	3	70.0–206.0	N	LM
11	84 05 26	37°01′N	164°02′E	19	145.0–230.0	G	SEM
12	84 06 02	37°00′N	158°00′E	114	38.0–125.0	N	SEM
13	84 07 16	42°00′N	172°00′E	7	213.0–282.0	G	SEM
14	84 10 06	43°09′N	153°14′E	5	300.0–330.0	D	SEM
15	85 05 20	36°00′N	150°00′E	3	21.0– 69.5	N	LM
16	85 05 21	38°15′N	149°59′E	2	8.3– 12.5	N	LM
17	85 05 23	38°30′N	152°00′E	2	26.5– 45.5	N	LM
18	85 05 24	38°00′N	152°00′E	9	29.0– 85.0	N	LM
19	85 05 29	38°45′N	156°00′E	3	16.0– 33.5	N	LM
20	85 05 29	38°30′N	156°00′E	2	27.0– 33.0	N	LM
21	85 05 29	38°15′N	156°00′E	3	24.6– 65.0	N	LM
22	85 05 30	38°00′N	156°00′E	3	31.5– 68.5	N	LM

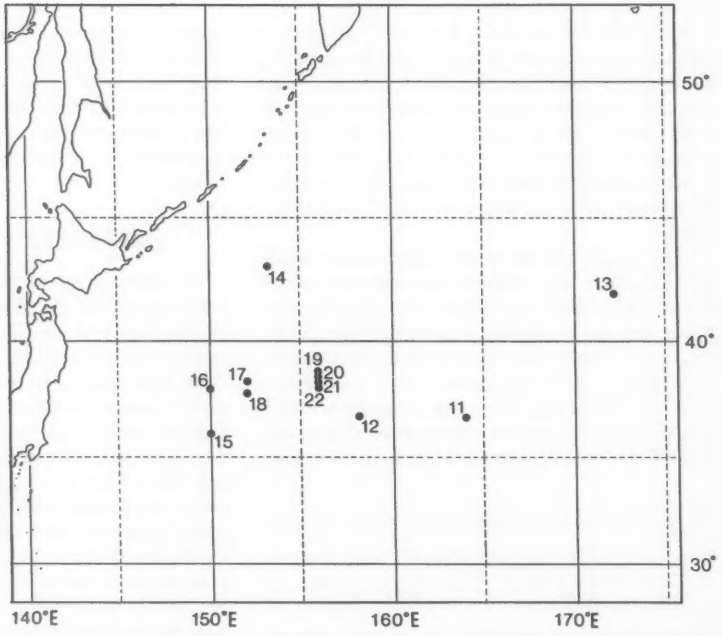


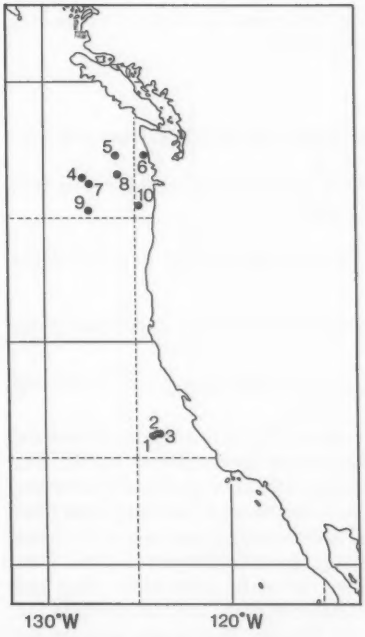
FIGURE 1.—Locations of Pacific saury collection in the North Pacific. Figures by

Sagittae were dissected out from fish and left to dry after removing tissues and membranes. We used a dissecting microscope with a polarizing filter to dissect otoliths from small larvae and juveniles. The otoliths were read either by light microscopy (LM) or by scanning electron microscopy (SEM). Otoliths that were to be read by LM were mounted in EUKITT[5] after dissection. Otolith radius was measured from the focus to posterior margin and the increments were counted along the same transect using the otolith reading system, which was developed by the Southwest Fisheries Center of the National Marine Fisheries Service, NOAA, and which consists of a light microscope, a video monitor, a micro-computer, and a digitizer (Methot 1981).

For SEM, otoliths were mounted in epoxy or methacrylate resin. The otolith radius was measured from the focus to the posterior margin with an optical comparator. The otoliths were ground oblique to the sagittal plane parallel to the long axis of the otolith in order to have a flat plane through the otolith nucleus. The polished surface was washed in xylene, using an ultrasonic washer, then dried and etched for 50 seconds with 0.2M EDTA-2Na (disodium ethylenediaminetetraacetic acid). The etched surface was coated with palladium platinum and observed under an SEM (JSM-25) at 15 kV.

The three authors of this paper read saury otoliths independently: the senior author read fish from the western Pacific up to 85 mm by LM, the second author read otoliths from the eastern Pacific by LM, and the third read otoliths from the western Pacific larger than 38 mm by SEM. To confirm that we were all interpreting the same structure as growth rings by SEM and LM, we compared 50 data points read by SEM and 14 points read by LM for western Pacific sauries between 38 and 85 mm. The distribution of increment number versus knob length was the same. We also checked for possible biases for the two readers using LM by having each read the same set of otoliths independently.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.



dots indicate sample numbers in Table 1.

RESULTS

The nucleus of a Pacific saury sagitta is approximately 20 μm in diameter and is composed of four to six small dense bodies which appear to be assemblages of calcareous spherules (Fig. 2a). These dense bodies are separated from one another and each is surrounded by a small concentric ring.

We observed the nucleus areas of otoliths from Pacific sauries collected in the western Pacific in 1985 (sample # 15–22) and found that most of them had a distinct ring of about 27 μm in radius. Between the nucleus and this distinct ring, four (or five) indistinct growth rings were detected (Fig. 2b).

We measured knob lengths of 27 larval and juvenile Pacific sauries before freezing and after thawing, and found that the ratio of these two measurements was 0.997. There was virtually no shrinkage by freezing and thawing. Theilacker (1980) found that preservation of larval northern anchovy, *Engraulis mordax*, in 80% alcohol did not cause additional shrinkage of the body after net treatment. Thus, knob lengths after both 80% alcohol preservation and freezing are comparable to each other, and this measurement corresponds to the size after net treatment. Since shrinkage factors by net treatment are not known for the saury, lengths are uncorrected for net shrinkage.

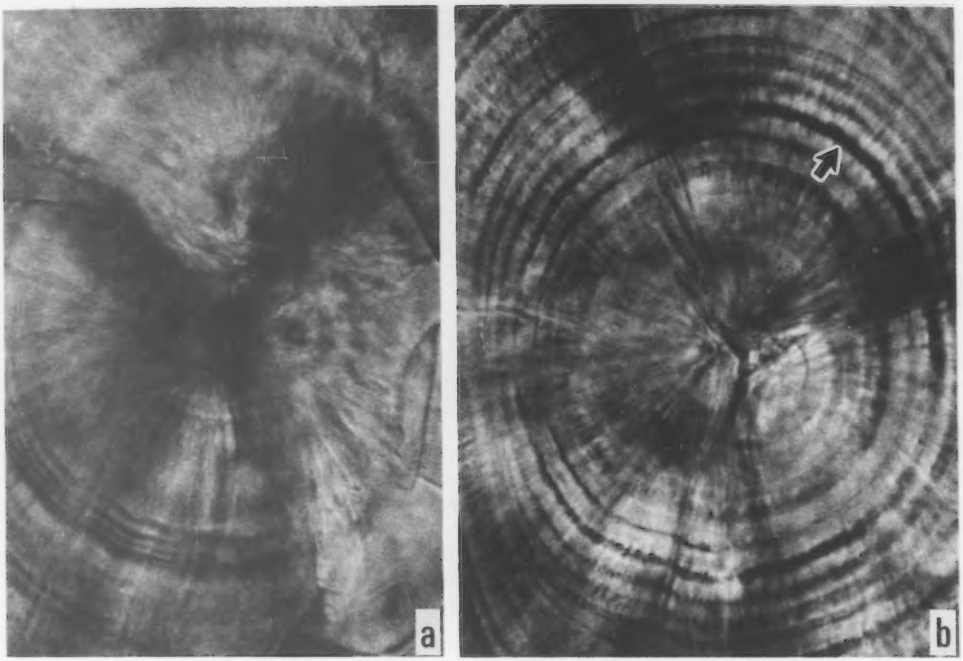


FIGURE 2.—Light micrographs of Pacific saury sagittae. a) Otolith nucleus composed of 5 or 6 separate dense bodies with surrounding cores. b) Assumed 4 embryonic and 1 hatching (arrow) rings.

The daily periodicity of growth increment formation in the Pacific saury has not been verified. For that reason we plotted the number of increments versus knob length instead of age versus length. We used the Laird-Gompertz equation to describe the relations of increment number and length as growth curves for both the eastern and western Pacific saury. Hatching size of artificially fertilized and incubated Pacific saury from the western Pacific was reported to be 7.19 mm in average live total length (Yusa 1960). From the drawing of a newly hatched larva in Yusa's paper, we estimated live knob length to be 6.60 mm. Shrinkage factors of northern anchovy in the size range from 6.00 to 7.99 mm were 0.90 for a 5-min net treatment and 0.85 for a 10-min net treatment (Theilacker 1980). Using these values, the capture size of a newly hatched larva of Pacific saury after a 5-min net treatment was estimated to be 5.95 mm and a 10-min treatment to be 5.61 mm. We fixed the hatching size from 5.85 to 5.95 mm in the growth curve, because the Pacific saury larvae at this size are in a more advanced developmental stage and shrank less by net treatment than northern anchovy.

The resulting growth equation for the eastern Pacific saury was

$$KnL = 5.85 \exp((0.0427/0.115)(1 - e^{(-0.0115(I-5))}))$$

and the equation for the western Pacific saury was

$$KnL = 5.95 \exp((0.0504/0.0128)(1 - e^{(-0.0128(I-5))}))$$

where KnL is a knob length in mm and I is the total number of increments observed in an otolith. The term, $I-5$, indicates that five increments were presumed to have been present at hatching. Data from the western Pacific saury appear to consist of two curves separated around 100 mm in KnL. Two Laird-Gompertz curves fit much better than one curve. The intersection of the two curves was at 114 increments and 100 mm. The growth equation for fish smaller than 100 mm was

$$KnL = 5.90 \exp((0.0865/0.0293)(1 - e^{(-0.0293(I-5))}))$$

and for fish larger than 100 mm KnL was

$$KnL = 3.01 \exp((0.0592/0.0126)(1 - e^{(-0.0126(I-5))}))$$

The estimated mean square error, 215.7, of the two curves was smaller than that for a single curve, 351.7. The two-curve model fits much better for the smaller size range up to 100 mm. The estimated mean square error of the two-curve model for this size range, 75.7, was much smaller than that of the one-curve model, 240.8.

The growth rate of Pacific saury in the eastern Pacific was slower than that in the western Pacific (Figs. 3, 4). The knob length of saury in the eastern Pacific would be about 75 mm at 100 rings, 170 mm at 200 rings, and 220 mm at 300 rings, whereas in the western Pacific knob length would be about 100 mm at 100 rings, 230 mm at 200 rings, and 300 mm at 300 rings. Assuming that the rings are formed daily, overall growth rates of the first one year of their life were 0.62 mm/d and 0.85 mm/d for the eastern and western Pacific Ocean, respectively.

The largest specimen examined was 330 mm from the western Pacific, which had 328 increments, and the oldest fish, also from the western Pacific, which measured 320 mm, had only 418 increments. These fish would be classified as very large or large by Novikov's categories of fish size composition (Novikov 1960, 1973). The largest fish examined from the eastern Pacific was 235 mm and had 241 increments. Hughes (1974), however, reported larger fish from the eastern Pacific.

In Pacific saury from the western Pacific, the relation between otolith radius in μm (OR) and knob length in mm (KnL) was linear on logarithm-logarithm coordinates (Fig. 5). The equation computed by the geometric mean regression (Ricker 1973) was

$$\ln (OR) = 2.33 + 0.749 \ln (KnL) \quad (r = 0.979).$$

The otolith radius at hatching (5.9 mm KnL) calculated by this formula was 38.9 μm, which was 12 μm larger than the radius of the presumed hatching ring.

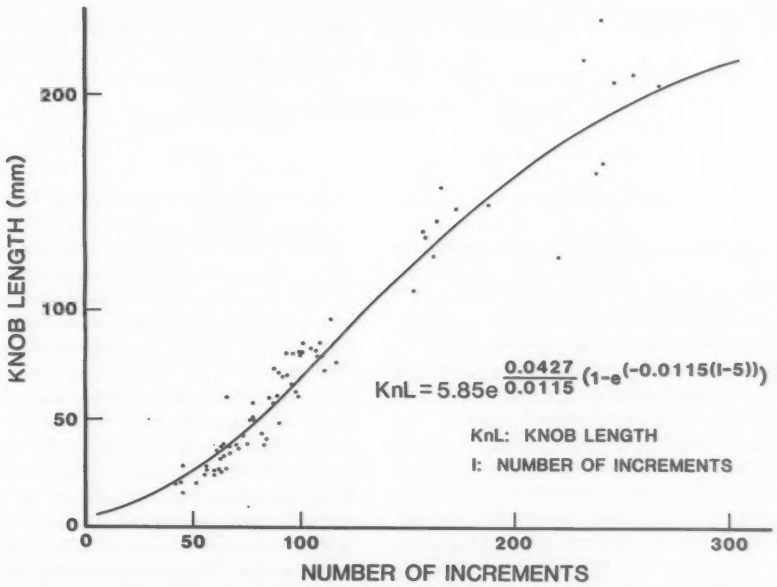


FIGURE 3.—Growth curve of the eastern Pacific saury.

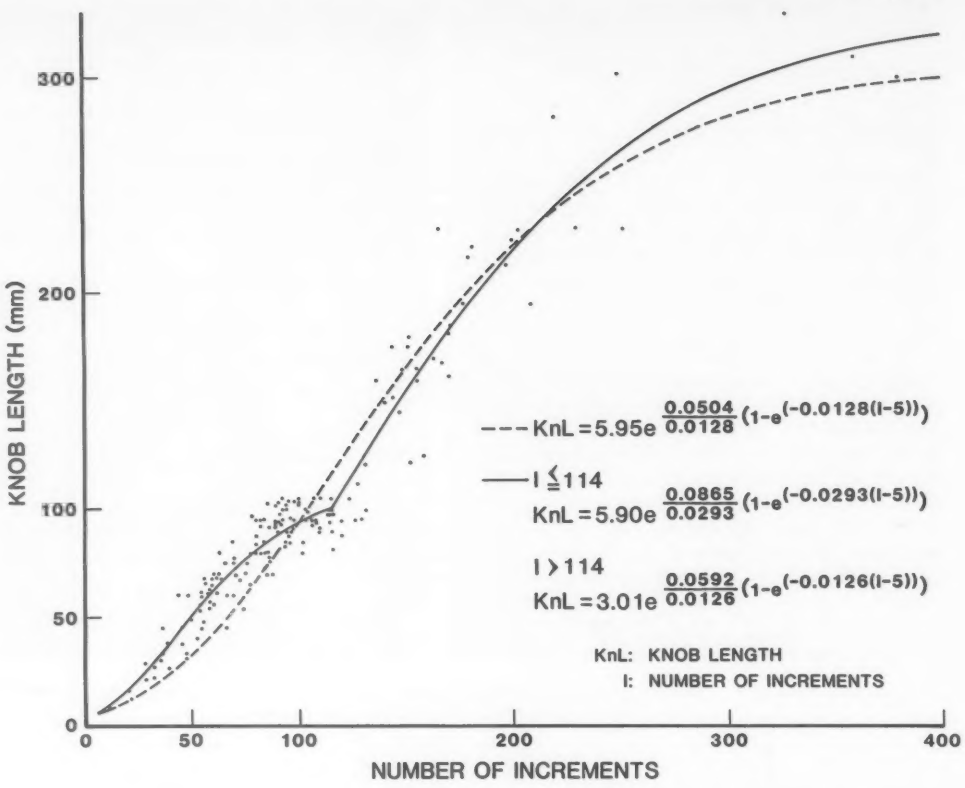


FIGURE 4.—Growth curve of the western Pacific saury.

DISCUSSION

The microstructure of otolith growth increments of the Pacific saury is similar to that of daily increments in some other fishes (Nishimura et al. 1985). Thus, the following discussion is based on the assumption that the increments are daily growth rings. A rearing experiment of larval sauries is under way in the senior author's laboratory to verify daily periodicity of the increment formation.

Formation of a few embryonic growth rings or a lamellar structure has been reported in California grunion, *Leuresthes tenuis*, (Brothers et al. 1976); mummichog, *Fundulus heteroclitus*, (Radtke and Dean 1982); and walleye pollock, *Theragra chalcogramma*, (Nishimura and Yamada 1984). Radtke and Dean (1982) mentioned that deposition of growth rings in the embryonic stage might be related to a long incubation period. Pacific saury has a long incubation period—about 17 days under 13.5°–15.7°C (Yusa 1960). At this temperature, eye pigmentation begins 7 or 8 days before hatching, and pectoral fins show constant movement from 5 or 6 days before hatching (Yusa 1960). Notochord flexion occurs about midway through embryonic development at 14°–22°C (Uchida et al. 1958). Thus saury is more advanced at hatching than killifish based on the embryonic development of killifish reported by Armstrong and Child (1965). Observing the central area of otoliths, we found four faint rings and a dark ring immediately outside of those rings. We assumed therefore that the four faint rings are embryonic rings and the dark ring is the hatching ring. This assumption may be confirmed by examining otoliths of late embryos and newly hatched larvae of saury.

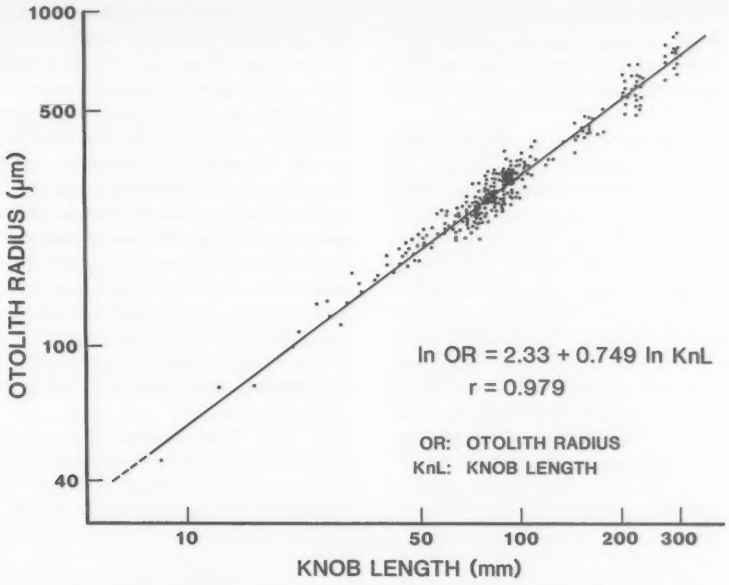


FIGURE 5.—Knob length and otolith radius relationship of the western Pacific saury.

Previous studies on age and growth of the Pacific saury have based on annuli on scales and/or otoliths. Sunada (1974) found five age groups in Pacific sauries off southern Oregon, California, and Baja California. Mean fork lengths of age groups were 171, 220, 246, 270, and 268 mm for age 0, 1, 2, 3, and 4, respectively. Hughes (1974) examined age composition of 5,248 sauries collected in waters off California up to Vancouver Island. He found spring- and autumn-born fish in his samples, but little difference was noted in growth rates between two groups. Approximate knob lengths of 1.0- to 5.0-year-old fish were 180, 230, 255, 290, 310 mm. The growth rates given in these two papers are not very much different. The saury grows at 0.5–0.6 mm/d up to 1 year old, which is almost equal to our growth rate in the eastern Pacific, 0.62 mm/d. Hatanaka (1955) found five age groups in the western population of the saury, 0–4 years old, and estimated mean body length of age groups to be 80, 160, 230, 265 mm for 1- to 4-year-old fish, respectively. Novikov (1960, 1973) divided sauries captured in autumn into five size groups, very small (–200 mm), small (201–240), medium (241–290), large (291–320), and very large (321+), and assigned the small, medium, and large to 1-, 2-, and 3-year-old with maximum 5-year-old fish.

A different model of Pacific saury growth in the western Pacific was proposed by Hotta (1960) based upon a hypothesis of two subpopulations. He separated the saury into spring-spawning and autumn-spawning populations based upon the observations of fish size composition, scales, otoliths, and numbers of vertebrae. He assigned four ages of half year intervals, 1.0, 1.5, 2.0, 2.5 years old, to fish 210–240, 260–280, 290–300, and 310–330 mm, respectively. The growth rate up to 1 year was 0.6–0.7 mm/d. Kim and Park (1981) examined Pacific sauries from Korean waters and found four size groups of four different ages of half-year intervals as well. They presented two growth models for each of two subpopulations, spring and autumn spawning, based upon the von Bertalanffy equation. The sizes at ages were almost identical to those of Hotta (1960). However, the hypothesis of two saury subpopulations in the western Pacific is not supported by electrophoretic analyses of genetic separation (Numachi 1971; Hara et al. 1982).

The average growth rate of the western Pacific saury in this paper was 1.1 mm/d from 0 to 8 or

9 months old. It was still faster than Novikov's growth rate of the corresponding age period (0.83 mm/d), which was the highest rate of all the previous reports. The fish would become 316 mm in one year according to our model.

Support for the fast growth rate of Pacific saury presented in this paper in the western Pacific can be found in rearing experiments. Hotta (1958) reared young sauries caught by a set net. He reared them in a crawl and fed them minced anchovy and mackerel twice a day. Young sauries 116 mm in mean length became 172 mm in the rearing period after 72 days. The growth rate was 0.78 mm/d. The sauries fed three times a day grew 130–143% faster than the group fed twice a day. Thus growth rates of young sauries may be higher than 1.1 mm/d (0.78 × 1.4 mm/d) when food is readily available. Our growth rate of sauries in this size range was approximately 1.5 mm/d in the western Pacific. For Atlantic saury, *Scomberesox saurus scombroides*, reared by Brownell (1983), the average growth rate of the larvae was 0.62 mm/d from hatching (7.5 mm SL) to 47-day old (36.8 mm SL). The growth rates of *Cololabis saira* in a corresponding period were 0.48 mm/d in the eastern Pacific and 1.0 mm/d in the western Pacific.

Our results indicate that the growth rate of Pacific saury in the western Pacific is much higher than in the eastern Pacific. This could be due to a difference in food availability between the two areas. However, mean zooplankton standing stock in 1951–66 was 34.8 g/m^2 in the California Current region in June (Smith and Eppley 1982), whereas that of Kuroshio water off southern Japan was 4.7 g/m^2 and of Oyashio area off northern Japan was 25.7 g/m^2 in May to July (Odate 1986). Thus, differences in zooplankton standing stock do not explain the difference in growth rates.

On the other hand, there seems to be a reasonable explanation for the reacceleration of growth rate at around 100 mm in the western Pacific saury. The western sauries hatch out mainly in offshore water of the Kuroshio Current (lat. 31–33°N) off Japan in winter. They migrate north to the Oyashio area (up to 46–50°N) where copepods are highly available. Young and adult sauries feed actively and gain fat. They are in the northward migration stage in early summer when they are about 100 mm, and are moving from poor Kuroshio water to rich Oyashio water (Fukushima 1979). High zooplankton standing stock in the Oyashio water and its derivatives might be responsible for the reacceleration of growth rate in fish older than 100 days.

The growth rates of Pacific saury in the western Pacific may differ from year-to-year due to environmental factors and may result in changes in size composition of the fish. Between 1968 and 1972, mean knob length of exploited sauries in the western Pacific was 170-250 mm, whereas in the 1980's the major mode in the size composition was 290-310 mm (S. Kosaka[6]). This increase could have been due to an acceleration of growth rate or a shift of spawning season to early months or both in recent years. The high growth rate of western Pacific saury presented in this paper has come from specimens collected in 1984 and 1985. The growth rate in the late 1960's and early 1970's may have been lower than that presented in this paper. Investigation of the interannual variation in growth rates using daily increments would distinguish between these two hypotheses.

We used three different gears to collect Pacific saury samples in the western Pacific. Knob lengths of sauries collected were from 8.3 to 125 mm by ring net, 145 to 282 mm by gill net, and 300 to 330 mm by stick-held dip net. Sauries of 125–145 mm might not be available either to the ring net or to the gill net. Further, the ring net may select small juveniles of a cohort in the size range over 100 mm, and this may have produced the two growth curves. This problem needs to be examined further with data on gear selectivity.

We do not know how long Pacific sauries survive after becoming adult. The oldest specimen in our sample was about 14 months old after hatching (418 increments). The largest saury aged (330 mm), which had 328 growth rings, is close to the maximum size. Although the maximum known length of the Pacific saury was reported to be about 400 mm (Hubbs and Wisner 1980), the largest fish exploited in Japan is about 340 mm. Therefore, the lifespan of the Pacific saury is about one year in the western Pacific. Our results are more consistent with those of Kosaka (1979) who found two age groups (0 and 1 year) than those (Sablin 1979) who found three age groups (0, 1, and 2 years).

In Japan, fishing efforts of the Pacific saury is regulated by fishing season as well as by the number of fishing boats. The fishing season starts in mid-August. Pacific sauries hatched in the main spawning season are about 250 days old at this time of year (approximately 270 mm) and are growing at the rate of 0.8 mm/d. Thus a 2-wk postponement at the beginning of fishing season would result in an 11 mm (10–15 g body weight) increase of average fish

[6]S. Kosaka, Tohoku Regional Fisheries Research Laboratory, Fisheries Agency, Shiogama, Miyagi 985, Japan, pers. commun.

length. The biomass and yield of Pacific saury need to be reestimated based on faster growth rates presented here.

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OTOLITH ULTRASTRUCTURE OF SMOOTH OREO, *PSEUDOCYTTUS MACULATUS*, AND BLACK OREO, *ALLOCYTTUS* SP., SPECIES

N. M. DAVIES,[1] R. W. GAULDIE,[1,2] S. A. CRANE,[1] AND R. K. THOMPSON[3]

ABSTRACT

The ultrastructure of sagittal otoliths from 14 *Pseudocyttus maculatus* and 25 *Allocyttus* sp. individuals were examined to determine their suitability for estimating age in these two species. Scanning electron microscopy revealed high levels of complexity in both external surface topography and internal structural organization in the sagittae of both species. Many different crystal forms were found, including calcite-like prisms. A close similarity in otolith structure exists between the two species. Deposition of check rings analagous to annual and daily growth increments was found to be irregular with the underlying complexity of crystalline growth obscuring the finer (analogous to daily) growth rings, making their periodicity difficult to validate and implying that with present techniques the sagittal otoliths of the oreo species *Pseudocyttus maculatus* and *Allocyttus* sp. are not suitable for age estimation.

The smooth oreo, *Pseudocyttus maculatus*, and the black oreo, *Allocyttus* sp., are two related species of the family Oreosomatidae. They are both important commercial species in New Zealand. The black oreo is the most commonly caught oreo in New Zealand waters, while the smooth oreo is the second-most commonly caught oreo. Little is known about the biology of these fish. The black oreo is endemic to New Zealand while the smooth oreo occurs in New Zealand, South Australian, South African, and South American waters (Last et al. 1983). In the waters south of New Zealand, the distributions of the two species overlap (McMillan 1985). The habitat range of the smooth oreo is between 650 and 1,200 m, and that of the black oreo is between 600 and 1,200 m (McMillan 1985).

A preliminary examination of the ultrastructure of otoliths [sagittae] of these fish was undertaken as part of a study to establish an ultrastructural basis for a suitable ageing technique. This study describes the external and internal structure and organization of the otoliths in terms of the suitability of the various check rings of the sagittae for age estimation.

MATERIALS AND METHODS

Three otoliths (the sagitta, astericus, and lapillus) are contained in the endolymphatic sac (Fig. 1a). The sagitta is the largest otolith and is located in the most ventral position in the sac. The arrangement of the three otoliths in the endolymphatic sac ranges between the primitive where a large astericus and sagitta with no lapillus is present (Gauldie et al. 1986) and the typical teleost arrangement where a small astericus is located close to the sagitta, and an even smaller lapillus is displaced into the atrium of the semi-circular canal. The oreosomatids are primitive fishes taxonomically, lying in the order Beryciformes (Nelson 1976), and the arrangement of otoliths reflects the taxonomic position of the fish. The orientation of otoliths described here refers to the orientation in situ. The lateral face is the outward (antisulcal) surface; the medial face is the inward (sulcal) surface. Investigation was restricted to the sagitta primarily because of the difficulties in establishing homologies for daily and annual type check rings in the astericus and lapillus.

Sagittae were dissected from 14 smooth and 25 black oreo individuals caught in bottom trawls off the east coast of New Zealand. These individuals ranged in length from 24.5 to 40.1 cm (black oreo) and 35.1 to 51.2 cm (smooth oreo).

Whole otoliths were photographed at 6× to 20× using a WILD[4] photomicroscope. The sagittae were embedded on glass slides in epoxy resin with the antisulcus surface uppermost and finely ground on a Struers Planapol-2 petrographic grinder. The

[1]Fisheries Research Centre, Ministry of Agriculture and Fisheries, Greta Point, Evans Bay Parade, P.O. Box 297, Wellington, New Zealand.
[2]To whom reprint requests should be sent.
[3]Electron Microscope Unit, Kirk Building, Victoria University of Wellington, Private Bag, Wellington, New Zealand.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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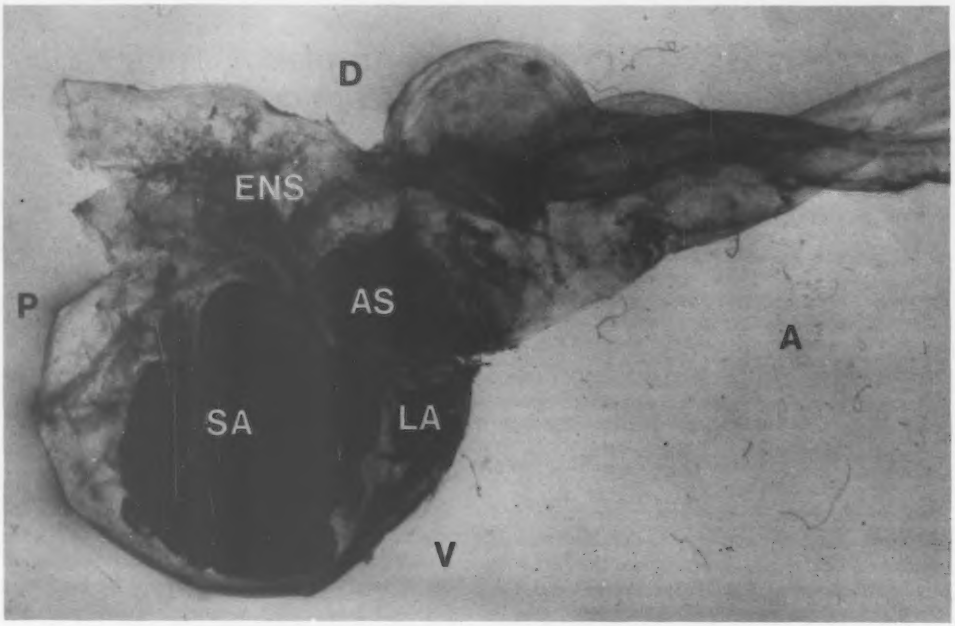

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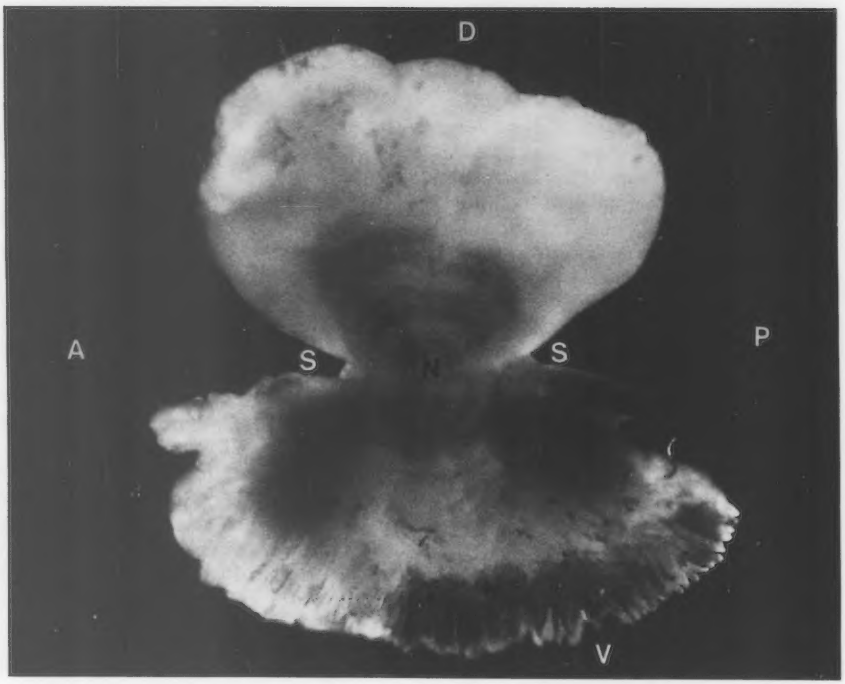

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FIGURE 1a.—Relative positions of the otoliths in the right endolymphatic sac (ENS) of the smooth oreo in lateral view: astericus (AS), lapillus (LA), and sagitta (SA). Anterior (A), dorsal (D), posterior (P), and ventral (V) surfaces are indicated. Magnification = 6.3×.

b.—Dorsal (regular) and ventral (irregular) lobes of the otolith in lateral view, nucleus (N), sulcus (S), and rest as in Figure 1a. Magnification = 12.5×.

c.—SEM of the lateral surface topography of the otolith. Scale bar = 1 mm.

ground surface was polished with 2000 grit wet and dry paper to yield a smooth surface for etching. The most successful results were obtained by etching with a 0.1 M solution of disodium salt of EDTA. The otoliths were immersed in this solution for 15 to 20 minutes. Other suitable etching solutions employed were 1) a 1% solution of HCl for 20 to 30 seconds and 2) a 2% solution of Histolab RDO (a commercial etching solution comprising a mixture of HCl and EDTA) for 5 minutes. A cellulose acetate peel was made of the etched surface to obtain an exact replica of the surface features. The peel was placed on a microscope slide under a cover slip, cleared with ethanol or distilled water, viewed, and photographed using a Zeiss photomicroscope. Direct observations of thin sections (about 20 μm) of otoliths did not show any more information than that observed in acetate peels. Acetate peels had the advantage of allowing successive grinds to be examined thereby avoiding the problem of losing information that might be located only in very narrow layers within the otolith.

Scanning electron microscope (SEM) photographs were taken of otoliths using a Phillips 505 SEM. Whole otoliths were glued on to SEM pin type mounts, cemented in position with contact cement, and sputter-coated with gold at approximately 5 Torr. The external surface topography of both the medial and lateral faces of the otoliths was photographed. Selected pieces of otoliths broken by thumb

pressure were examined and photographed to obtain internal structural information. Finely ground cross-section surfaces were also polished and etched for examination with the SEM.

RESULTS

Smooth Oreo Otolith

The sagitta is clearly divided into two distinct structures: a small, smooth, regular dorsal lobe and a larger, irregular ventral lobe (Fig. 1b). The irregular lobe has branched crystal formations and clefts at the ventral edge. The lateral face topography is complex (Fig. 1c). The central bumpy area contains the nucleus between the two lobes. Radiating outwards from the nucleus are concentric ridges on the antisulcul surface.

The crystal morphology of the lateral surface of the sagitta is variable. Over much of the central parts of the sagitta, large and variably oriented crystals give a coarse appearance to the surface of the otolith (Fig. 2a) which presumably obstructs, by diffraction, potentially clear zones in the whole otolith viewed by transmitted light. At the edge of the regular lobe, the crystal type alters to form slabs of crystal layers (Fig. 2b). The analogous area on the irregular lobe yields variable crystalline structures with complex alignments (Fig. 2c). Deep troughs and branching furrows break up the crystal forms at the edge of the irregular lobe.

The medial surface has three distinct parts: the central sulcal area, the edge of the irregular lobe, and the edge of the regular lobe (Fig. 3a). Raised ridges and two prominent knobs are found in the central sulcal area. Crystals compacted into a petal-like growth pattern are found in this part of the otolith (Fig. 3b). Contrasting to this, more porous crystal structures occur in the edge areas of the regular lobe (Fig. 3c). Further variety is found on the irregular lobe, where a very porous, honeycomb-like crystal arrangement exists (Fig. 3d). At the

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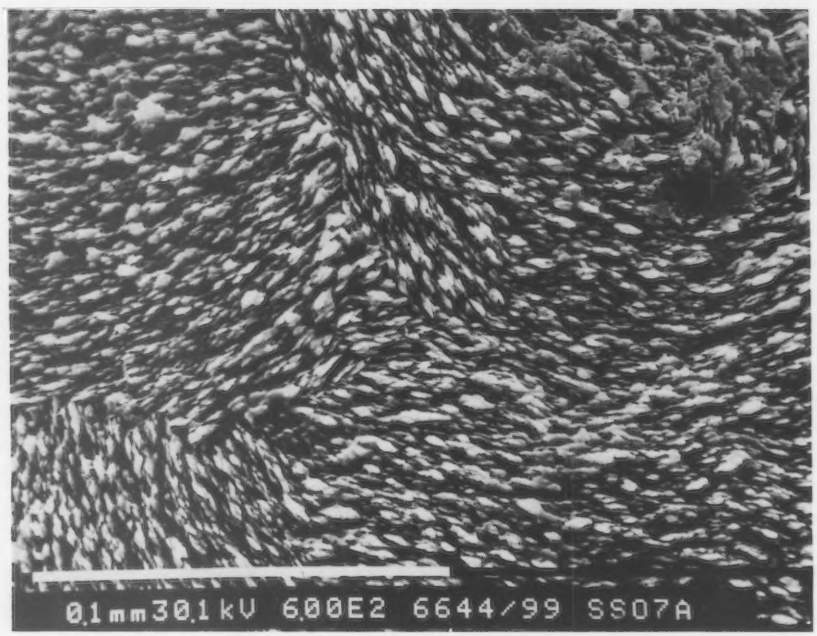
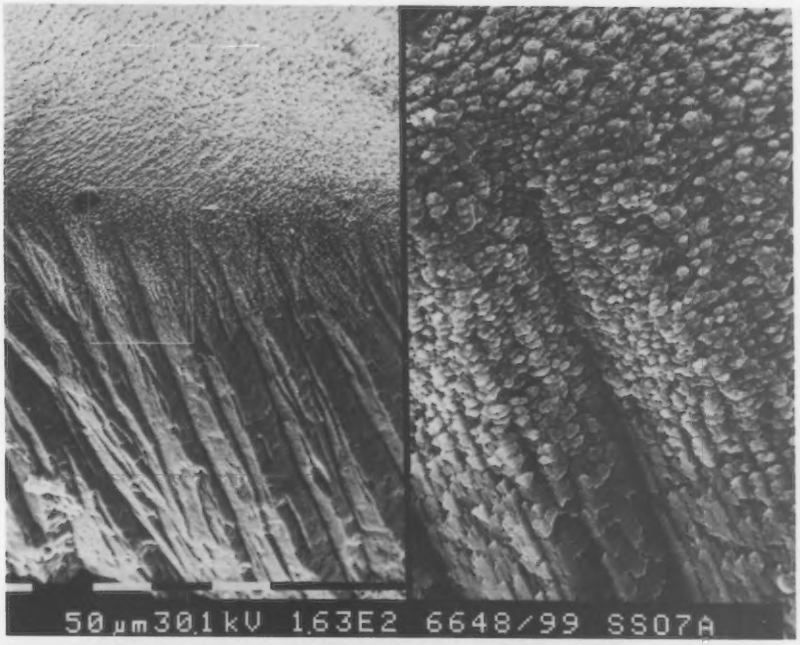


FIGURE 2a.—Coarse crystal structure of the central lateral surface of the smooth oreo otolith. Scale bar = 0.1 mm.

b.—Split-screen SEM of the transition of the crystal-type at the edge of the lateral surface of the regular lobe. Magnification = 163× and 652×.

c.—Haphazard crystal alignments at the edge of the lateral face of the irregular lobe. Scale bar = 0.1 mm.

b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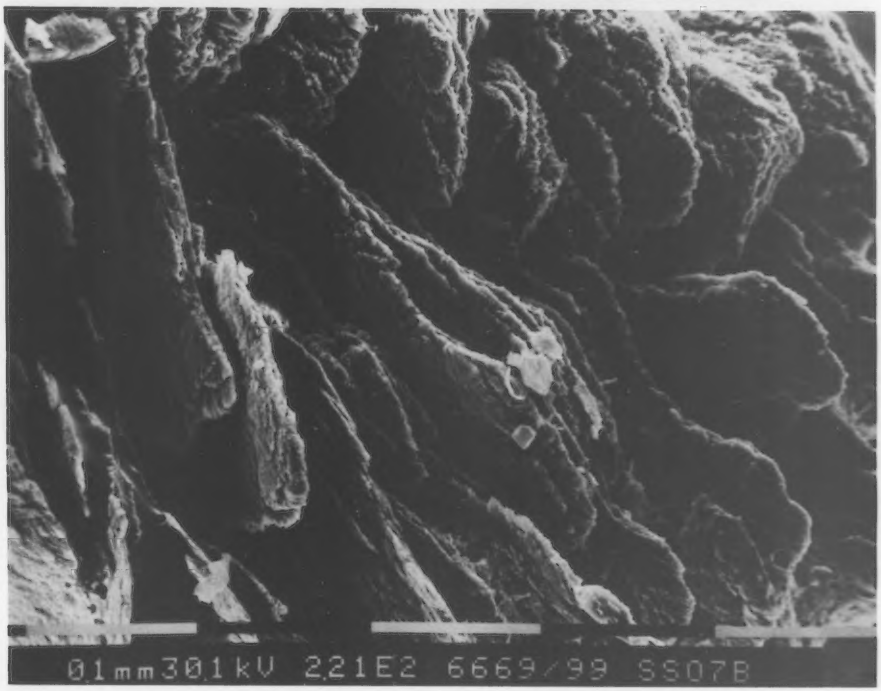
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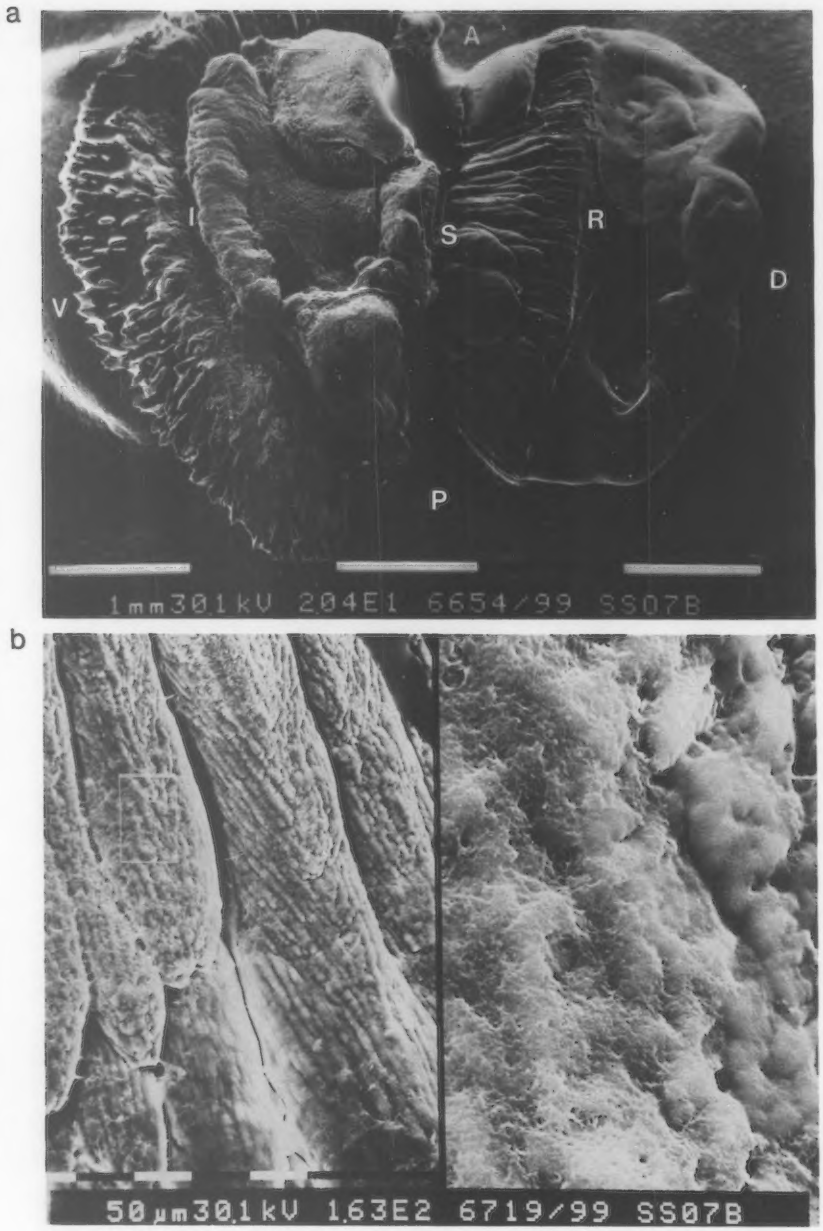

FIGURE 3a.—Medial view of the smooth oreo otolith showing the irregular lobe (I), regular lobe (R), and sulcus (S). Scale bar = 1 mm.

b.—Split-screen SEM of petallike crystal growth in the sulcus on the medial surface. Magnification = 163× and 1141×.

c

d

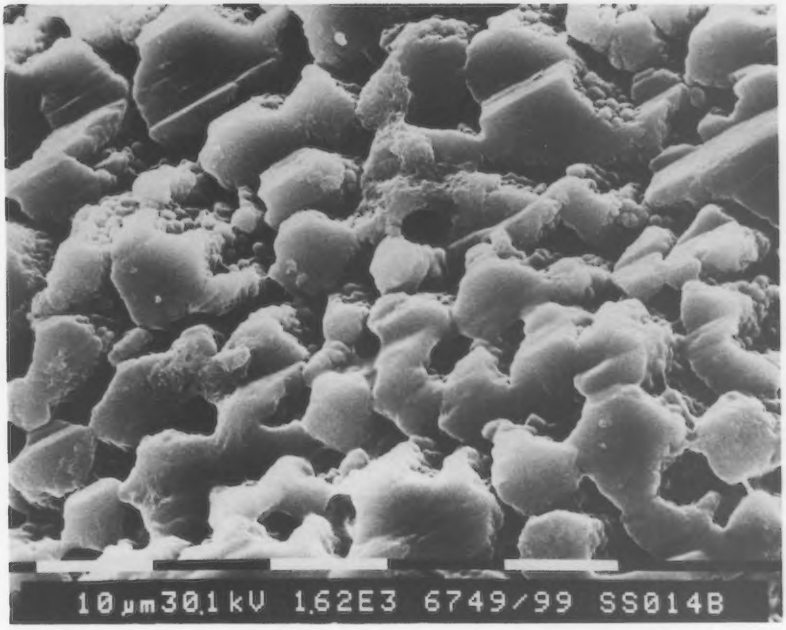

FIGURE 3c.—Porous crystals on the medial surface of the regular lobe. Scale bar = 10 µm.
d.—Honeycomblike crystal structure on the medial surface of the irregular lobe. Scale bar = 10 µm.

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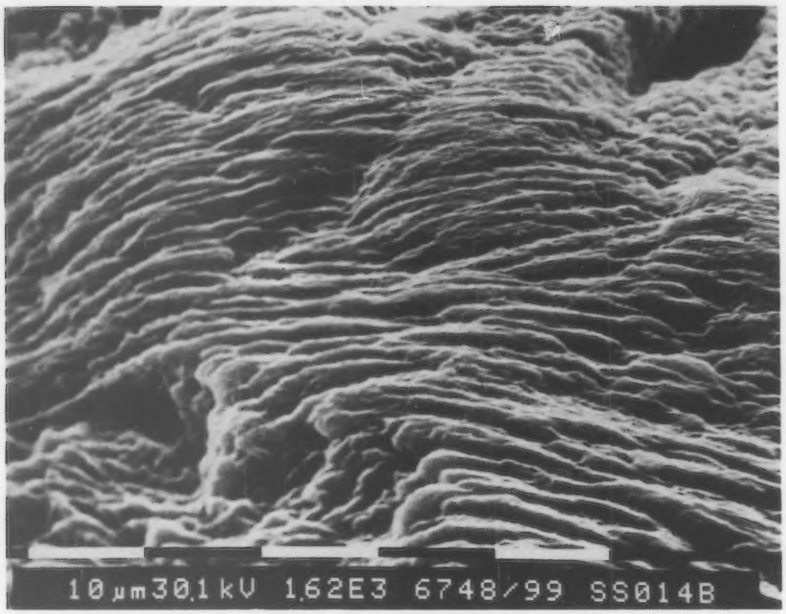


FIGURE 3e.—A laminar pattern of crystalline growth on the medial face of the irregular lobe. Scale bar = 10 µm.

edge of this lobe, a laminar crystalline growth pattern develops, adding to the overall variation of crystal structures on the medial surface (Fig. 3e). Other studies of otolith ultrastructure present the otolith as homogeneous in crystal form, composed almost entirely of monoclinal aragonite crystals (Degens et al. 1969). The complex crystallinity of the oreo otoliths resembles that of the mollusc shell, which, although aragonitic, often has a pattern of complex variation in crystal habit (Carriker et al. 1980).

Within the broken otolith, the nucleus lies at the center of a spherical primordium (Fig. 4a). Crystals grow outwards from the primordium and epitaxial (Degens 1976) growth patterns exist (Fig. 4b). Complex leaf-shaped crystals occur in areas directly beneath the lateral surface of the fractured irregular lobe (Fig. 4c). Beneath the medial surface, a remarkable series of hexogonal crystals of calcite occur as large rectangular blocks embedded *within* the otolith (Fig. 4d). Calcitic prisms have been described in molluscs as resulting from the regeneration of broken shells (Watabe 1983). It is difficult to imagine otoliths being broken and regenerated in situ.

Major and minor check rings similar to those described (Gauldie 1987) for otoliths from the orange roughy, a deepwater species from the same habitat, occur (Fig. 4e). When polished and etched, the check rings become clearly visible with deep etched checks occurring between the less deeply etched checks analagous to microscopic growth increments in other species (Fig. 4f). At a higher magnification the finer increments become obscured by the coarseness of the underlying crystal type (Fig. 4g). Those fine increments that are visible occur irregularly and have varying widths.

Large-scale rings analogous to opaque/hyaline annual zones were observed in the regular lobe. The mean width of these zones, measured using transmitted light (Fig. 1b), was 0.34 mm ($\pm$0.06). The concentric ridges observed by SEM on the lateral surface of the regular lobe (Fig. 1c) have a mean width of 0.27 mm ($\pm$0.06). These two structures, opaque/hyaline zones and surface ridges, have about the same width with no statistically significant differences between them.

Examination of otolith cross sections reveals widely spaced, large rings with many finer rings in between (Fig. 4h). When examined in greater detail, the demarcation between the large and finer rings

a

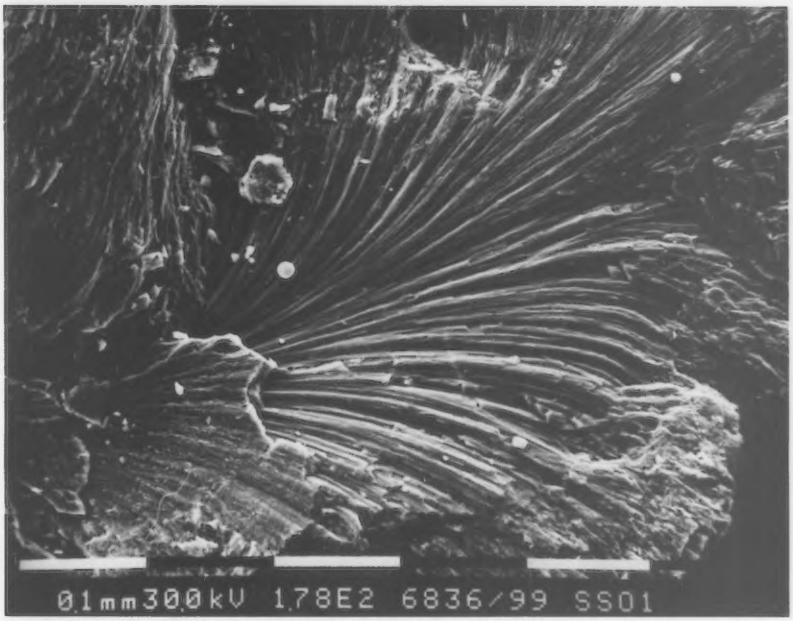
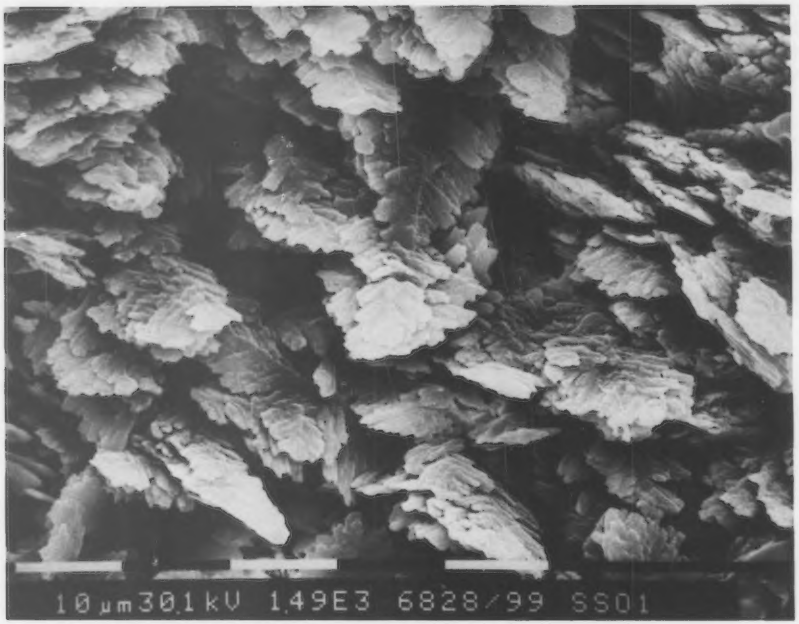


FIGURE 4a.—Broken smooth oreo otolith reveals the spherical primordium (PM) and nucleus (N) and the surrounding radial crystal growth. Scale bar = 0.1 mm.

b.—Epitaxial crystal development in the broken otolith. Scale bar = 0.1 mm.

c



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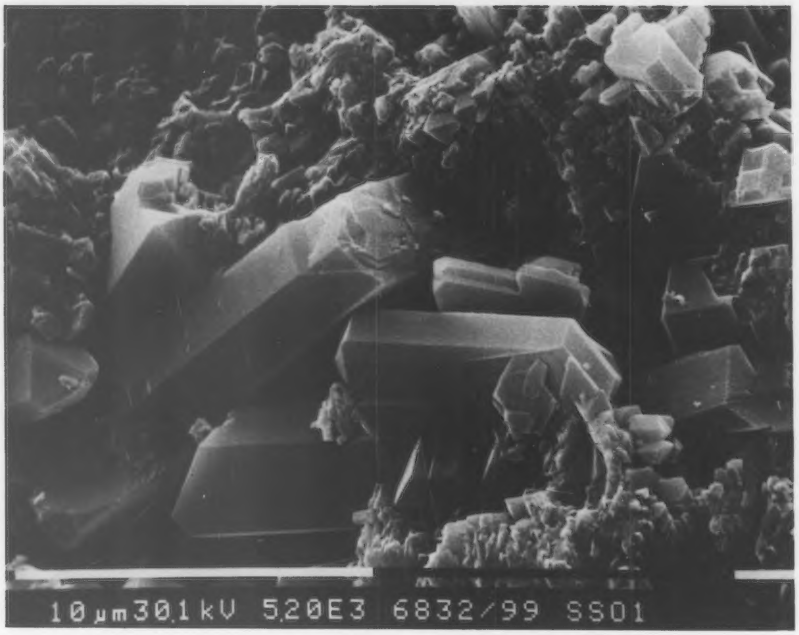


FIGURE 4c.—Leaf-shaped crystals beneath the lateral surface of the broken otolith. Scale bar = 10 µm.
d.—Calcitic prism crystals beneath the medial surface of the broken irregular lobe. Scale bar = 10µ.

e

f

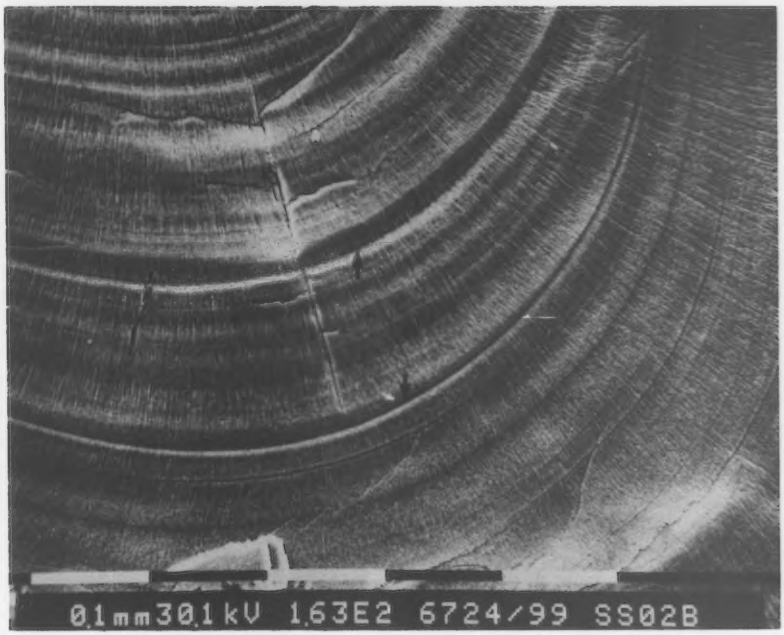
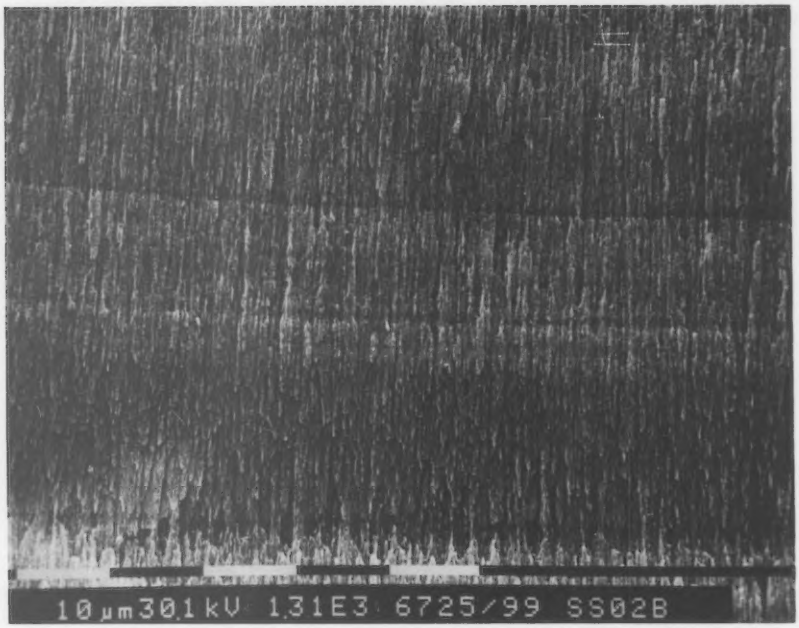


FIGURE 4e.—Discontinuous uniform crystal growth forming rings in the broken otolith. Scale bar = 0.1 mm.
f.—Fine and deep (arrowed) increments on the polished and etched otolith surface. Scale bar = 0.1 mm.

g



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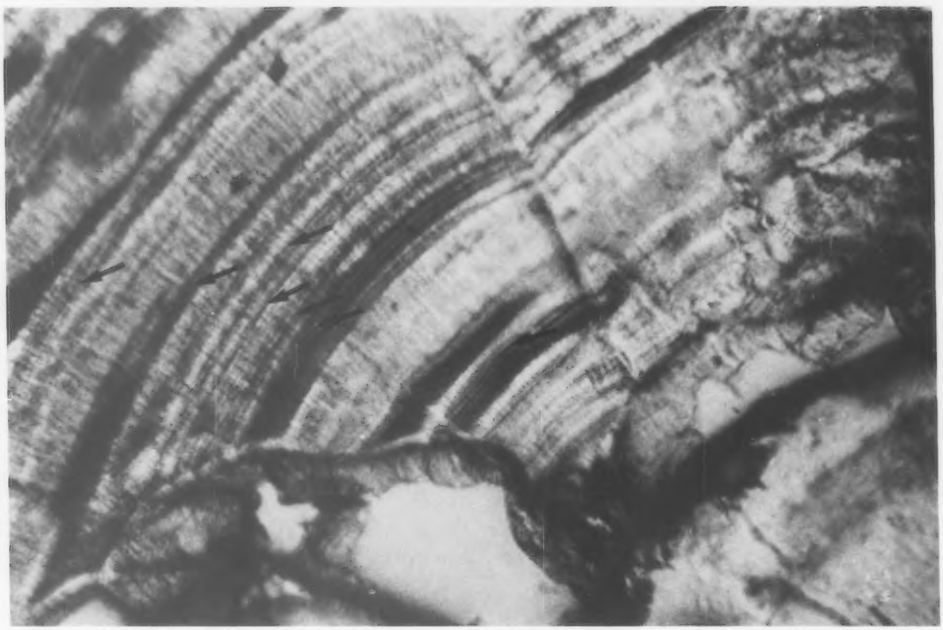


FIGURE 4g.—Fine increments obscured by coarse crystallinity on the polished and etched otolith surface. Scale bar = 10 µm.
h.—Fine increments (arrowed) found between widely spaced large rings in the otolith cross-section. Magnification = 72×.

i

j

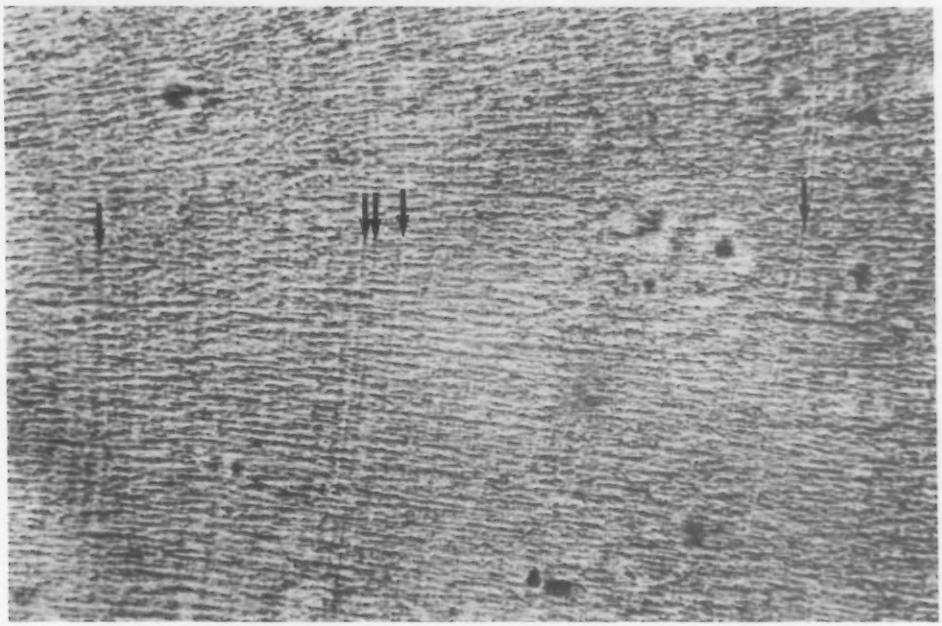


FIGURE 4i.—Variation of increment widths (arrowed) in the otolith cross-section. Magnification = 160×.

j.—Cellulose-acetate peel showing the intermittency of fine increment sequences (arrowed), often obscured by a coarse underlying crystallinity. Magnification = 160×.

becomes difficult to determine because of the intermittent nature of the growth increments and the variety of width-sizes (Fig. 4i). In large areas of the otolith, increments appear to be absent or indeterminate, with a coarse underlying crystal structure (Fig. 4j) making accurate determination of increment sequences difficult. However, the fine increments of the oreo otolith are 3 to 5 μm wide, which is within the range of daily growth increments described for other species (Jones 1986; Gauldie in press).

Black Oreo Otolith

The black oreo otolith is almost identical to that found in the smooth oreo in overall shape, proportion, structure, topography, surface and internal crystallinity, and increment pattern. Some minor differences do, however, exist.

In the medial sulcus, the prominent knobs found in the smooth oreo otolith are smaller than in the black oreo. On the surface of the sulcus, large leaflike crystals having various orientations occur (Fig. 5a). Also present in the sulcus are porous, sponge-like crystals adjacent to membranous structures (Fig. 5b). Smooth patches, where crystals appear absent, occur on the lateral surface of the otherwise coarsely crystalline irregular lobe (Fig. 5c). At higher magnification the smooth patches are seen to be smaller growth forms of the larger adjacent crystals.

DISCUSSION

Despite some minor differences in topography and crystallinity, the sagittae of both species are essentially identical. The otoliths are structurally complex with a great variety of crystalline forms. The coarse

a

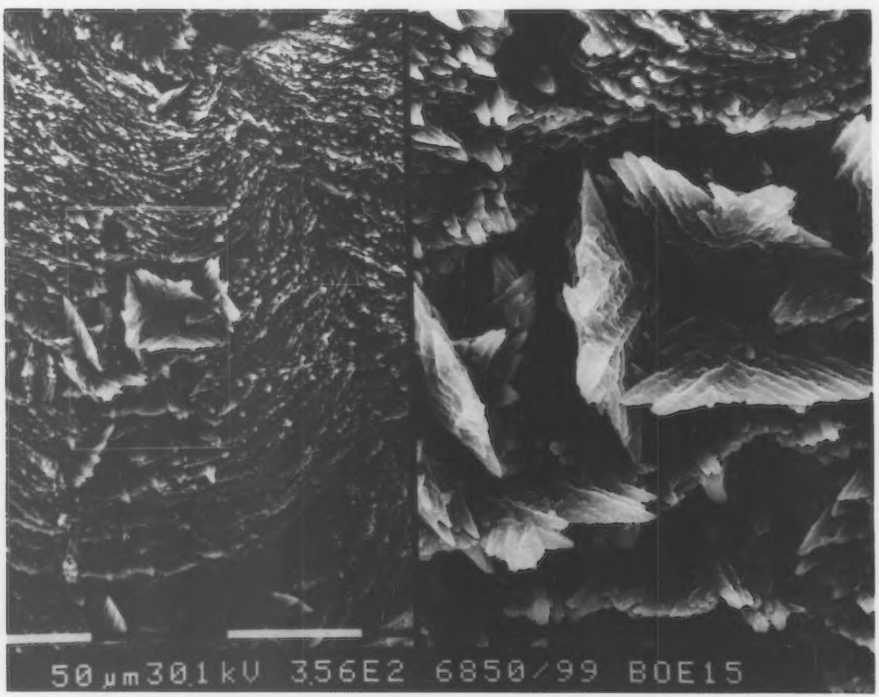
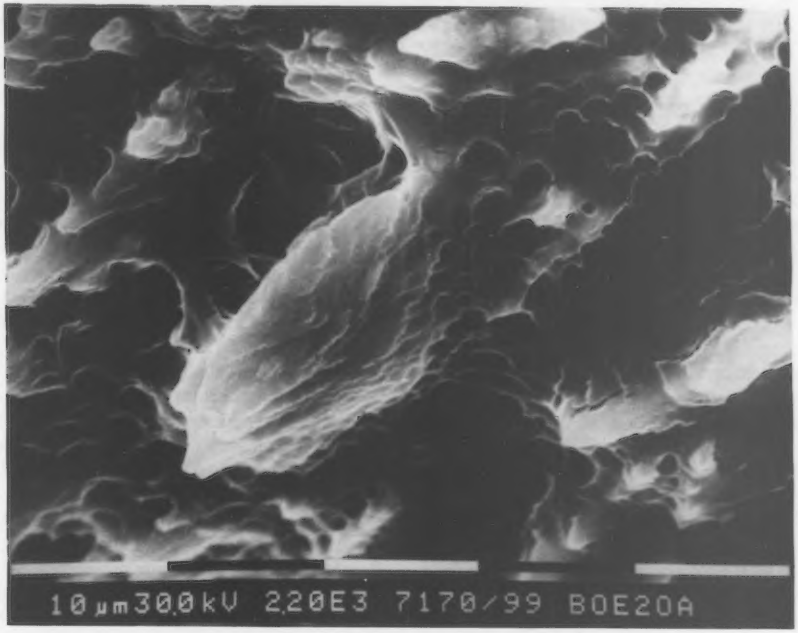


FIGURE 5a.—Split-screen SEM of large leaflike crystals in the black oreo otolith sulcus. Magnification = 356× and 979×.
b.—Porous, sponge-like crystals in the otolith sulcus. Scale bar = 10 μm.
c.—Smooth patches on the central lateral surface of the otolith. Scale bar = 0.1 mm.

b


10µm30.0kV 2.20E3 7170/99 BOE20A

c

0.1mm30.0kV 1.70E2 7172/99 BOE20A

crystals on the central lateral surface are comparable with those in the oyster shell described as individual laths (Carriker et al. 1980). The leaflike crystals in the sulcus of the black oreo otolith are similar to the chalky crystal forms in the oyster shell (Carriker et al. 1980). Such a variety of crystalline forms is uncommon in teleost otoliths. The low legibility of structures of various kinds in the otolith may reflect this complex crystallinity. However, the complex crystallinity of the mollusc shell is thought to reflect changes in both the external and internal milieu of the organism (Wilbur and Saleuddin 1983). Thus the difficulties of reading the oreo otolith in the conventional sense may be offset by the life history record (albeit difficult to translate) provided by its complex crystallinity.

The broken sections of the otolith reveal the internal structure organization, and development of crystals. Epitaxial crystal growth in the oreo otolith results in columnar, monoclinal crystals of aragonite. However, the presence of calcite-like prisms has not been described for other otoliths. Calcite occurs on the antisulcal surface of some otoliths apparently by simple crystallization out of the fluid of the endolymphatic sac (Morales-Nin 1985), but calcite has never been described from within an aragonite otolith (Carlstrom 1963). In molluscs, calcite replacement of aragonite results in an orderly alignment of calcite crystals following the alignment of the original aragonite crystals. The disorderly appearance of the calcite-like hexagons in the smooth oreo otolith may be due to a diagenetic transformation of aragonite to calcite with depth. The compensation depth for the aragonite/calcite transformation is about 3,000 m (Fyfe and Bischoff 1965) well beyond the known range of the smooth oreo which has a maximum recorded depth of 1,300 m. However, there may be enough variation in either the kind or amount of stabilizing protein in the smooth oreo otolith to allow crystal changes to occur at shallower depths than 3,000 m.

The complex, and often coarse, crystal structure of the oreo otolith obscures the sequences of increments when they do occur. As a result, large rings observed at low magnification become indistinct at higher magnification when many finer increments appear. The large rings could be assumed to be annual check rings, but the difficulties in differentiating between the fine and large rings create ambivalence in one's interpretation. The finer microscopic growth increments, analagous to daily growth rings, have no uniform width and occur intermittently making accurate counting impossible.

The suitability of an otolith for determining the age of a fish depends on the pattern of both annual and daily check rings inferred from the structure of the otolith. The hyaline/opaque zones observed in the regular lobe (using transmitted light) had a similar mean width to the concentric ridges found by SEM on the lateral surface. The *t*-statistic we obtained accepts the null hypothesis that no significant difference exists between the two means. Mel'nikov (1981) regarded these opaque/hyaline zones as annual check rings in the otolith of *Allocyttus verrucosus*. However, because no evidence exists for a relationship between the surface ridges and fish age, it is possible that Mel'nikov's (1981) ages are incorrect. Furthermore, the width of the opaque/hyaline zones (0.34 mm) would indicate daily growth increments less than 1 μm wide. There are no reports in the literature of validated daily growth rings of such small size. In addition, the microscopic growth increments which we have observed in the oreo otolith are 3 to 5 μm wide, which is a size range commonly observed in other species.

With the techniques available we have been unable to use either annual- or daily-type structures to develop a technique for age estimation for *Pseudocyttus maculatus* and *Allocyttus* sp. The reasons for these difficulties may lie in the crystal morphology of the otoliths which are more complex than any so far described in the literature.

ACKNOWLEDGMENTS

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RELATIONSHIP BETWEEN SEDIMENT CHARACTER AND SEX SEGREGATION IN ENGLISH SOLE, *PAROPHRYS VETULUS*[1]

D. SCOTT BECKER[2]

ABSTRACT

English sole, *Parophrys vetulus*, were collected by otter trawl in the nearshore zone of Puget Sound, Washington, during two surveys conducted in 1981–82 and 1984. Stations in both surveys were distributed across a broad range of sedimentary environments. Sex segregation by English sole was strongly associated with the grain-size characteristics of bottom sediments. This association was persistent across a variety of sampling conditions, including different years, seasons, embayments, and depths. Fish age did not appear to influence the observed association. Results of this study provide the first documentation of the influence of sediment character on sex segregation by a pleuronectid, and suggest that this relationship should be considered in future studies of English sole and, perhaps, other pleuronectids as well.

Sex segregation by fishes of the family Pleuronectidae (i.e., righteye flounders) has been documented for numerous species from the United States (Alverson and Chatwin 1957; Fadeev 1970; Alton 1972), Europe (Rae 1965), and Asia (Moiseev 1953; Kovtsova 1982). These patterns have been related to such factors as geographic location, depth, season, and age of fish. However, because most of these observations have been made while fishes were being collected for other purposes, the underlying reasons for the observed patterns are poorly understood.

Several studies have documented sex segregation in English sole, *Parophrys vetulus*, a pleuronectid found in nearshore areas along the west coasts of the United States and Canada (Hart 1973). In describing the catch of the English sole fishery in Hecate Strait, British Columbia, Ketchen (1956) noted that considerable sex segregation takes place, particularly during the summer months. In a study of the population characteristics of this species in Puget Sound, Holland (1969) found a difference of 18% between the percentages of males in the populations from two locations. Because both of these accounts were largely anecdotal, no evaluations of the observed patterns were made.

One factor that has yet to be evaluated with respect to sex segregation by pleuronectids is the character of bottom sediments. Because pleuronectids live in close association with the sea floor, it might be surmised that the characteristics of that environment exert a differential influence on the distributions of the two sexes. Additional support for this hypothesis comes from the fact that the influence of sediment character on the overall distribution (i.e., both sexes pooled) of several pleuronectids has been well documented (Ketchen 1956; Alverson et al. 1964; Feder et al. 1974; Pearcy 1978; Scott 1982; Becker 1984).

In this paper, I evaluate patterns of sex segregation by English sole in relation to the character of bottom sediments in nearshore areas of Puget Sound, WA. This study provides the first determination of how sediment character influences sex segregation in a pleuronectid. In relating sediment character to sex segregation in English sole, I also evaluate the potential influences of depth, season, and fish age on the observed relationships.

METHODS

English sole were sampled during two independent surveys conducted in several embayments of Puget Sound in 1981–82 and 1984. The relationship between sex segregation and sediment character was evaluated separately for each survey. Although the two surveys differed with respect to such variables as station locations, sampling times, and sample sizes, the basic collection and analytical methods used in both surveys were similar.

In both surveys, the sex ratio of the English sole captured at each station was represented by the proportion of the sample comprised of males (i.e., male proportion). Sediment character at each station was represented by the percentage (by weight) of the

[1]Contribution No. 759, School of Fisheries, University of Washington, Seattle, WA 98195.

[2]School of Fisheries, University of Washington, Seattle, WA 98195; present address: PTI Environmental Services, 3625 132nd Ave. S.E., Bellevue, WA 98006.

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grain-size distribution comprised of fine-grained material (i.e., <0.063 mm in size). This variable was used as an index of sediment character because many physical, chemical, and biological characteristics of sedimentary environments covary with the grain-size distribution (Buchanan 1984).

During 1981–82, English sole were collected from 15 May to 6 July 1981 at 12 transects in Commencement Bay, Elliott Bay, and Sinclair Inlet (Fig. 1). Fishes also were collected during three additional time periods (23–24 November 1981; 8–9 March 1982; 30–31 August 1982) to evaluate seasonal patterns at three stations in Commencement Bay (CB-1, CB-4, and CB-5; Fig. 1). These stations were selected to represent a gradient of sediment grain size. Although the seasonal sampling occurred over a 2-yr period, it was assumed that interannual variation was not sufficiently large to obscure major seasonal patterns.

During the May–July sampling, English sole were collected at each transect during morning (07:00–09:30), midday (10:00–13:30), evening (20:30–23:30), and midnight (00:30–04:00). During the remaining sampling periods, fish were collected only during midday and evening. For each transect, results obtained for different periods of the diel cycle were pooled before male proportions were calculated. Sex determinations and evaluations of spawning condition were made for all English sole larger than 160 mm total length (TL). Age was not determined.

During 1984, English sole were collected from 4 to 9 June 1984 at 15 transects in Commencement Bay and at 2 transects in Carr Inlet (Fig. 1). Sampling was conducted during daylight hours (06:30–17:00) at all transects. Sex determinations and evaluations of spawning condition were made for all individuals larger than 225 mm TL. Age was determined by otolith analysis for all fish.

During both surveys, English sole were collected using a 7.6 m (headrope) Marinovich otter trawl having a body mesh of 3.2 cm (stretched) and a cod end liner mesh size of 0.8 cm (stretched). Trawling was conducted along isobaths at a constant vessel speed of approximately 2.5 knots.

During both surveys, bottom sediments were sampled using a modified van Veen bottom grab and the grain-size distribution of the top 2 cm of sediment was determined using standard sieve and pipette techniques (Folk 1968). During 1981–82, sediments were collected at five sampling points located at approximately equal distances along each transect. During 1984, sediments were collected at a variable number of stations located within 300 m from each transect.

The association between percent fine-grained sediment and male proportion of English sole was tested using Spearman's rank correlation coefficient (r_s). The association between station depth and male proportion was tested in the same manner. Differences in male proportion among age-classes of fish and among the seasonal sampling transects were tested using the G-test (Sokal and Rohlf 1981).

RESULTS

Station depth, percent fine-grained sediment, sample size, and male proportion at each transect from the 1981–82 and 1984 surveys are presented in Tables 1 and 2, respectively. During 1981–82, 4,430 English sole were sampled from stations ranging in depth from 8 to 36 m. Percent fine-grained sediment ranged from 5.8 to 92.1% and male proportion ranged from 0.20 to 0.91. During 1984, 1,007 English sole were collected from stations ranging in depth from 5 to 20 m. Percent fine-grained sediment ranged from 8.6 to 87.5% and male proportion ranged from 0.13 to 0.98.

The correlation between percent fine-grained sediment and male proportion of English sole was significant ($P \leq 0.01$; $r_s = 0.73$) for the May–July sampling of the 1981–82 survey (Fig. 2). This correlation was also significant ($P \leq 0.001$; $r_s = 0.80$) for the 1984 survey (Fig. 2). Correlations between depth and male proportion were not significant ($P > 0.05$) for either the 1981–82 ($r_s = -0.10$) or 1984 ($r_s = -0.04$) survey.

For the stations sampled seasonally in 1981–82 (CB-1, CB-4, and CB-5), heterogeneity of male proportion among stations was significant ($P \leq 0.05$) during all four sampling periods (Fig. 3). In all cases, male proportion was lowest at CB-5, highest at CB-4, and intermediate in magnitude at CB-1. This gradient of increasing male proportion was consistent with the gradient of increasing percent fine-grained sediment at the three stations (Table 1). The mean abundance of English sole at the three stations rose from a minimum level in March to a peak in May–July, and then declined through August to a level in November that was similar to that in March (Fig. 3).

For both surveys combined, 64 (1.2%) English sole were found to be in spawning condition. Twenty-four of those individuals were collected during March, to represent a spawning component of 14.8% during that month. The remaining 42 individuals were sampled between May and July to represent

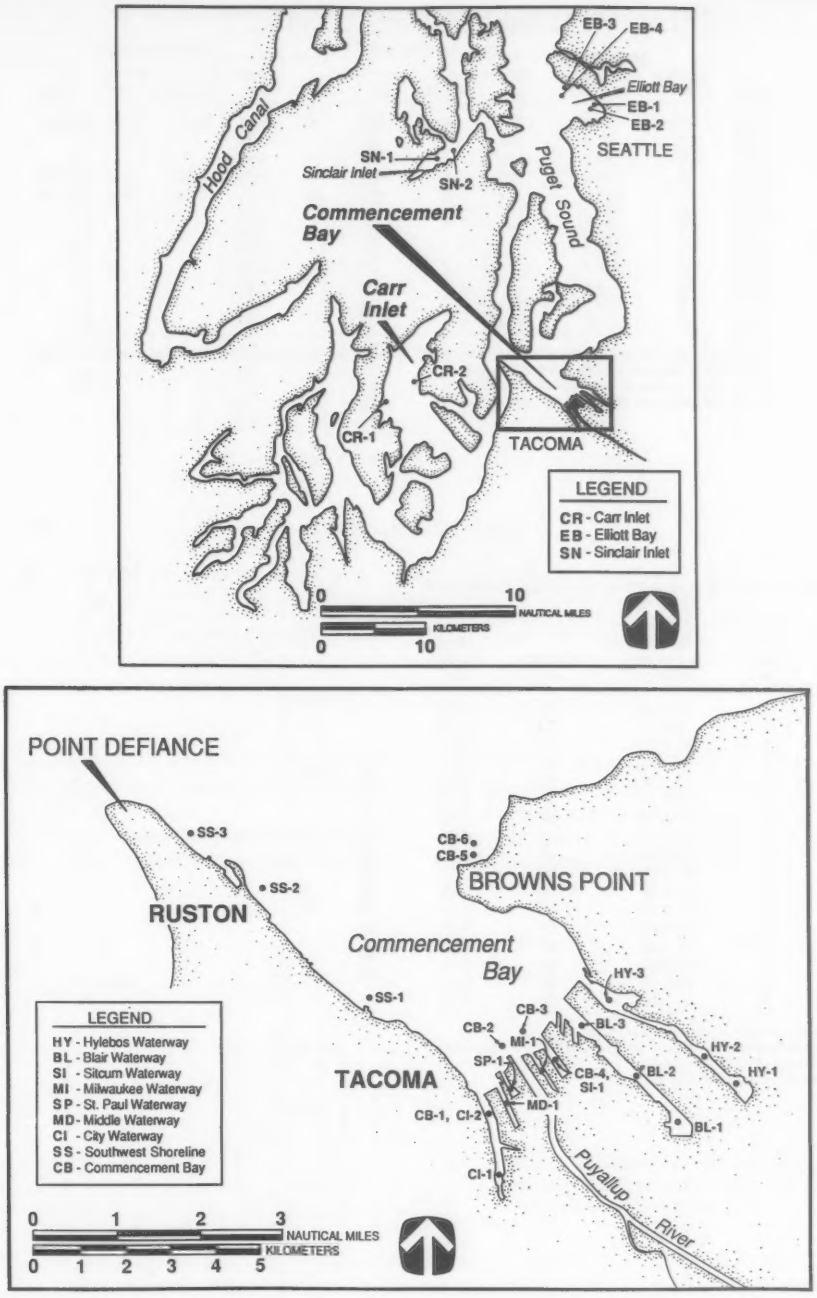

FIGURE 1.—Locations of transects sampled in 1981–82 (denoted by CB, EB, and SN) and 1984 (all remaining transects).

TABLE 1.—Characteristics of transects and samples of English sole during 1981–82.[1]

Station[2]	Depth (m)	Mean percent fine-grained sediment[3]	Sample size[4]				Male proportion			
			May–July	August	November	March	May–July	August	November	March
CB-1	10	27.1	655	249	65	90	0.83	0.74	0.58	0.57
CB-2	33	47.0	554				0.78			
CB-3	36	44.2	160				0.79			
CB-4	14	71.6	589	146	174	38	0.91	0.82	0.77	0.87
CB-5	13	7.6	181	67	68	35	0.55	0.64	0.44	0.20
CB-6	35	11.2	128				0.66			
EB-1	14	56.0	82				0.68			
EB-2	31	76.2	17				0.76			
EB-3	16	5.8	90				0.53			
EB-4	32	8.8	49				0.49			
SN-1	8	92.1	683				0.84			
SN-2	10	13.7	310				0.30			

[1]Sampling in May–July and November was conducted in 1981, whereas sampling in August and March was conducted in 1982.
[2]Locations of transects are presented in Figure 1.
[3]Each value is based on five replicate samples.
[4]All English sole were larger than 160 mm TL.

TABLE 2.—Characteristics of transects and samples of English sole during 1984.

Station[1]	Depth (m)	Mean percent fine-grained sediment[2]	Sample size[3]	Male proportion
CR-1	18	14.5 (2)	60	0.28
CR-2	12	8.6 (2)	60	0.13
SS-1	9	18.2 (2)	59	0.29
SS-2	10	22.9 (6)	60	0.48
SS-3	20	8.7 (6)	60	0.35
CI-1	5	68.8 (4)	57	0.75
CI-2	9	58.2 (4)	52	0.73
MD-1	6	40.4 (2)	59	0.42
SP-1	5	48.9 (3)	60	0.77
MI-1	10	87.5 (5)	60	0.87
SI-1	12	73.8 (5)	60	0.98
BL-1	11	55.2 (1)	60	0.77
BL-2	12	74.3 (9)	60	0.88
BL-3	10	55.4 (6)	60	0.88
HY-1	9	68.1 (5)	60	0.45
HY-2	9	79.8 (7)	60	0.80
HY-3	9	61.1 (12)	60	0.73

[1]Locations of transects are presented in Figure 1.
[2]Number of stations used to calculate mean percent fine-grained sediment at each transect is given in parentheses.
[3]All English sole were larger than 225 mm TL.

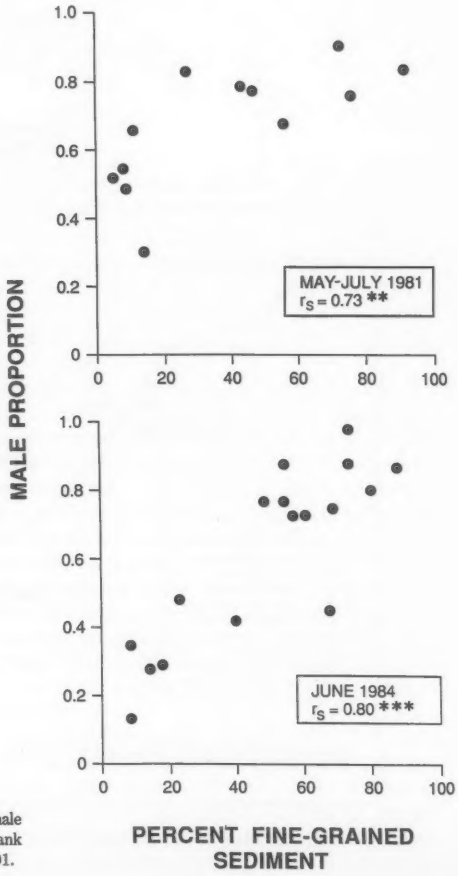

FIGURE 2.—Comparison of percent fine-grained sediment and male proportion of English sole populations using Spearman's rank correlation coefficient (r_s). ** = $P \leq 0.01$, *** = $P \leq 0.001$.

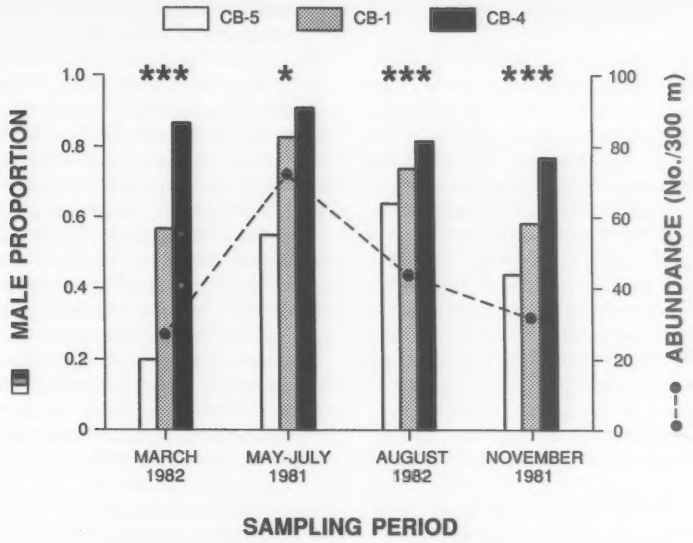

FIGURE 3.—Comparisons of male proportion of English sole populations at three Commencement Bay stations during four sampling periods using the *G*-test. Mean abundance of English sole at all three stations is plotted for each sampling period. The values of percent fine-grained sediment at Stations CB-5, CB-1, and CB-4 were 7.6%, 27.1%, and 71.6%, respectively. * = $P < 0.05$, *** = $P < 0.001$.

a spawning component of 0.9% during that period. No fish were found to be in spawning condition during August and November.

For English sole aged 3–10 years old during the 1984 study, male proportion for each age-class ranged from 0.50 to 0.66 (Fig. 4). However, the heterogeneity among age-classes was not significant ($P > 0.05$). Nineteen fish aged 2 or >10 years old were not included in this analysis because sample sizes by age-class were too small.

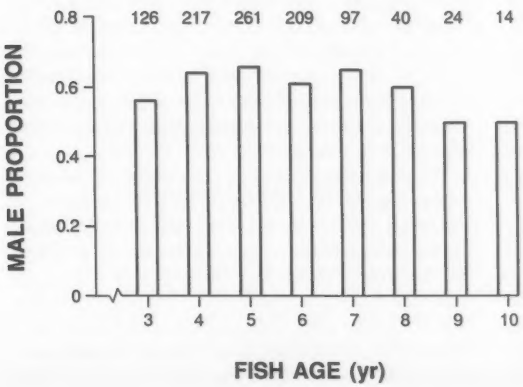

FIGURE 4.—Comparison of male proportion among age-classes of English sole collected in 1984. Sample size is presented above each bar.

DISCUSSION

Results of this study demonstrate that sex segregation by English sole in nearshore areas of Puget Sound is strongly associated with the grain-size distribution of bottom sediments. In addition to the results of statistical analyses, the strength of this association is demonstrated by its persistence across a variety of sampling conditions. For example, the association was found in two independent surveys conducted 2–3 years apart. Furthermore, the 1981–82 survey represented an analysis of large-scale patterns across three embayments, whereas the 1984 survey focused on small-scale patterns within a single embayment. The association between sex segregation and sediment grain size also persisted across seasons and across a range of depth.

Although a significant association was found between sediment grain size and male proportion of English sole, a variety of factors that covary with sediment grain size may have been partly or totally responsible for this association (Lagler et al. 1977; Moyle and Cech 1982). Examples of physical/chemical variables that often covary with grain size and may influence fish distributions include depth, current speed, turbidity, and dissolved oxygen. Examples of biological factors include the composition of prey assemblages and the distribution of predators. Although results of this study demonstrated that depth did not influence the observed association between sediment grain size and male proportion, further experimentation is required to identify the factor or suite of factors that directly influences sex segregation in this species.

Despite the fact that depth did not influence the patterns of sex segregation identified for English sole, the range of depth considered in this study (5–36 m) is a small fraction of the total range occupied by this species (0–550 m; Hart 1973). It therefore is possible that depth-related sex segregation in this species may be observed if a wider range of depths were examined. For example, considerable sex segregation by depth was found for Dover sole, *Microstomus pacificus*, off the west coast of the United States when a large depth range (110–440 m) was evaluated (Hagerman 1952; Alton 1972).

Based on results of the 1984 survey, no relationship between age and male proportion in English sole was evident. It therefore is unlikely that age influenced the observed relationship between male proportion and sediment grain size. A decline in male proportion with increasing age has been found for several pleuronectids (Rae 1965; Kovtsova 1982). Because most of the fish examined in this study were relatively young (<8 years old) compared with the maximum age of 15–17 years sometimes reached by individuals of this species (Ketchen 1956; Holland 1969; Van Cleve and El Sayed 1969), consideration of older fish may alter the patterns observed in this study. Although sample sizes for fish aged 9–10 years were relatively small in this study, male proportion in those age groups (0.50) was lower than that observed in all younger age groups (0.57–0.66).

The season of sampling did not alter the observed relationship between male proportion and sediment grain size. This relationship remained intact despite the fact that the mean abundance of English sole changed substantially throughout the seasonal cycle. The observed seasonal changes in mean abundance are consistent with the seasonal pattern of migration exhibited by adults of this species and most other pleuronectids. That pattern includes a migration to deeper water in the fall for overwintering and spawning, and a return migration to shallower water in spring for feeding throughout the summer (Ketchen 1956; Alverson et al. 1964; Roff 1982). It is unlikely that spawning substantially influenced the observed seasonal patterns of sex segregation in English sole, because the largest percentage of fish in spawning condition during any season was <15%. However, sex segregation in relation to spawning in pleuronectids has been documented for several species (Moiseev 1953; Alverson and Chatwin 1957), and may influence sex segregation in English sole when a substantial percentage of the population is in spawning condition.

Results of this study suggest that the influence of sex segregation should be considered when characteristics of English sole populations are compared among habitats that differ with respect to sediment character. Patterns based on population characteristics capable of exhibiting a dependence on sex (growth, condition, disease prevalence, tissue contamination) could be strongly biased if differences in the sex ratio among stations are not considered. This concern should probably be extended to studies of other pleuronectids, because the relationship between sex segregation and sediment character is unknown for most species.

Although the reasons for the observed patterns of sex segregation in English sole are unknown, a potential explanation is that different energetic needs induce male and female fish to utilize different habitats. Female English sole grow to a larger size than males and mature at an older age (Ketchen 1956; Holland 1969; Van Cleve and El-Sayed 1969; Hart 1973). In addition, fecundity in females is proportionate to individual size (Ketchen 1956; Hart

1973). These patterns are found for numerous pleuronectids and are thought to allow females to outgrow predators and maximize fecundity (Roff 1982). Female English sole may therefore select different habitats than males to support their differential reproductive requirements. Because many characteristics of benthic macroinvertebrate assemblages (i.e., the primary prey of English sole) are related to sediment character (Gray 1974; Rhoads 1974; Pearson and Rosenberg 1978), selection of habitats that differ in sediment grain size provides females with different prey spectra and energetic potentials than are available to males. In addition, differential habitat selection would reduce the potential of competition for food between sexes.

In summary, sex segregation by English sole was strongly associated with the grain-size characteristics of bottom sediments. This association was persistent across a variety of sampling conditions, including different years, seasons, embayments, and depths. Fish age did not appear to influence the observed association. Results of this study provide the first documentation of the influence of sediment character on sex segregation in a pleuronectid, and suggest that this relationship should be considered in future studies of English sole and, perhaps, other pleuronectids as well.

ACKNOWLEDGMENTS

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OCCURRENCE OF *CANCER* CRAB (*C. MAGISTER* AND *C. OREGONENSIS*) MEGALOPAE OFF THE WEST COAST OF VANCOUVER ISLAND, BRITISH COLUMBIA

GLEN S. JAMIESON AND ANTAN C. PHILLIPS[1]

ABSTRACT

The seasonal and cross-shelf occurrences of *Cancer* crab (*C. magister* and *C. oregonensis*) megalopae in 1985 along a transect line perpendicular to the coast off Tofino, British Columbia, are presented. Megalopae of both species were generally absent from surface waters during daylight hours. The two species may have slight temporal differences in nocturnal surface abundance, with *C. magister* occurring later in the evening and earlier in the morning than *C. oregonensis*. Their relative occurrence at the surface during the night was used to calibrate cross-shelf megalopal abundance data. Cross-shelf megalopal intermolt stage proportions were calculated, relating degree of megalopal development to proximity of nearshore habitat required for successful settlement of larvae.

Cancer magister megalopae were present from April to August, with peak abundance in May and June. Megalopae were abundant in a broad band 37–148 km from shore, with peak abundance (2,871 10 m^{-2}) 56 km offshore in June. In May, some late stage megalopae were collected in coastal inlets but settlement appeared low in coastal study areas. Megalopal abundance decreased abruptly shoreward of 28 km from the coast.

Cancer oregonensis megalopae were also present from April to August, with their pattern of cross-shelf abundance basically similar to that of *C. magister*. However, in contrast to *C. magister*, abundance of late stage megalopae in coastal inlets was relatively high (313 10 m^{-2}) in June, indicating that a significant settlement of megalopae of this species could have occurred.

Evidence for cross-shelf movement of *Cancer* megalopae is discussed.

Dungeness crab, *Cancer magister*, range from the Aleutian Islands to northern Mexico in the eastern Pacific (Hart 1982) and are commercially exploited from northern California to Kodiak Island, AK. As part of an ongoing study of Dungeness crab recruitment off the west coast of Vancouver Island, the abundance and distribution of larvae off Tofino, British Columbia, are being studied to determine how variability in annual recruitment is affected by larval settlement.

Dungeness crab larvae are planktonic and pass through five zoeal stages and one megalopal stage before settling to the sea bottom. Studies of larvae prior to the 1970s primarily involved descriptions of larval morphology (Mir 1961; Poole 1966), and it was not until Reed (1969) developed laboratory culture methods that larval environmental requirements were first described. Optimal ranges of temperature and salinity for laboratory-cultured zoeae were 10.0°–13.9°C and 25–30‰ respectively, but their survival was not significantly affected by the temperature and salinity ranges occurring in the waters off Oregon, where Reed's study was conducted, at the time of year when larvae are commonly found. Lough (1976) suggested offshore larval movement would allow larvae to avoid lower nearshore salinities, and that normal oceanic salinity levels probably favor survival over the long term.

The temporal occurrence of larvae in open coast oceanic waters varies somewhat according to latitude, with larvae present earliest in the season in the southern part of the species' range. Seasonal occurrence has not been well documented in the inshore waters of Georgia Strait, Puget Sound, and Juan de Fuca Strait, but appears to differ significantly from that in open coast waters. Larval settlement, which typically occurs in May and June off the outer coast of Washington, can occur as late as mid-September in northern Puget Sound (D. Armstrong[2]).

Temporal and spatial distributions of crab larvae have been documented for the years 1975–80 in the Gulf of Farallones and the San Francisco-San Pablo-Suisun Bay complex in central California (Reilly

[1]Department of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, B.C., Canada V9R 5K6.

[2]D. Armstrong, University of Washington, Seattle, WA 98195, pers. commun. December 1986.

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1983) and for the years 1969–70 along a transect off Newport, OR (Lough 1975, 1976). These studies suggest that while larvae are hatched in the nearshore, shallow-water environment preferred by adult Dungeness crab, they subsequently move alongshore and offshore, and then inshore, often over considerable distances. Larvae hatched off California and Oregon in late winter have been hypothesized to move northward with the Davidson Current before its reversal in March-April, and offshore as a result of upwelling, Ekman transport, estuarine runoff, and geostrophic flow, depending on location and season (Lough 1976; Wild and Tasto 1983). Later stage zoeae are typically found progressively further offshore, and it seems to be the megalopal stage that returns inshore (Lough 1976; Reilly 1983). The megalopal stage is the strongest swimming stage (Jacoby 1982), but there is no direct evidence to indicate that their inshore movement is active.

There are five species of crabs of the genus *Cancer* in British Columbia (Hart 1982), and larvae of *C. oregonensis* also occur in abundance in offshore waters along with *C. magister* (Lough 1975). *Cancer oregonensis* has no commercial importance, but since it occurs with *C. magister*, data on both species of crabs are included in this study. Comparisons of occurrence between the two species may provide insight into possible environmental mechanisms or processes that influence transport from offshore areas to the inshore juvenile habitats, which the larvae of both species must reach.

This study establishes the seasonal and spatial occurrences of *Cancer* megalopae along a transect over and beyond the continental shelf off the west coast of Vancouver Island (Fig. 1). The geographical area is of particular interest because of the location of a major regional crab fishery near Tofino (Jamieson 1985; Noakes and Jamieson 1986) and the resulting importance of understanding factors influencing the magnitude of local larval crab settlement. The oceanography off Vancouver Island has been relatively well studied (Freeland et al. 1984; Thomson 1981), and because of the intrusion of Juan de Fuca Strait waters into the general longshore oceanographic regime and the relative increase in topographical complexity of the continental shelf, it is considerably more complicated than that found

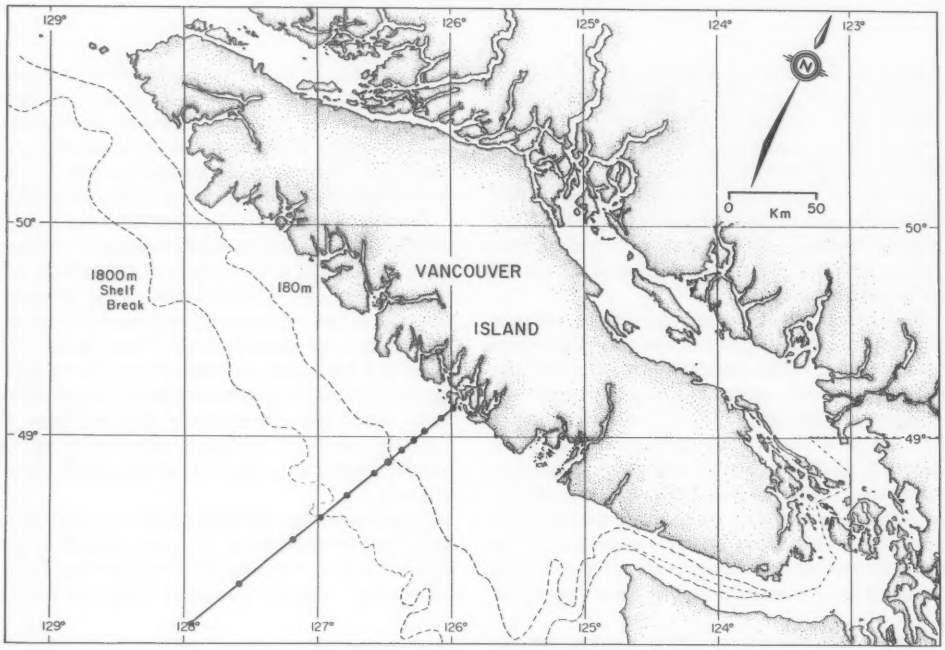


FIGURE 1.—The survey transect line, with stations, over which this study was conducted.

south of Cape Flattery (Hickey 1979). Along the eastern Pacific coast, Cape Flattery marks a significant change in nearshore oceanography, and this study to investigate larval crab distribution in open coast waters is the first one north of this landmark.

GENERAL OCEANOGRAPHY OFF VANCOUVER ISLAND

A seasonal surface current moving northward from about lat. 32°N to 51°N (northern Vancouver Island) typically exists in nearshore waters from October to March (Fig. 2). South of Cape Flattery, this is called the Davidson Current (Hickey 1979) whereas off British Columbia, it appears to consist of two components. Nearshore, there is the year-round, northward flowing Vancouver Island Coastal Current, about 20–30 km wide, and further offshore, there is the seasonal Shelf-Break Current, perhaps a continuation of the Davidson Current, which reverses direction in response to changes in the large-scale wind field (Freeland et al. 1984). The Davidson Current off Oregon has an average northward flow of 50 cm/s for 30% of the time (Boisvert 1969), sufficient to transport larvae significant distances northward during their developmental period if they remained continuously in the current. The California Current is a seasonal, southward moving, surface current of similar magnitude and location to the Davidson Current. It occurs off Vancouver Island (Hickey 1979) in the spring and summer, along with the seasonal, southward flowing, Shelf-Break Current on the outer continental shelf (Freeland et al. 1984). These currents could transport larvae located off Vancouver Island during the spring and summer southwards (Fig. 2). North of Vancouver Island, outer continental shelf currents are poorly described, but off Cape St. James (southern tip of the Queen Charlotte Islands), the surface flow is strongly southward almost year-round, turning northward only in March and April (Freeland et al. 1984). The Vancouver Island Coastal Current originates at the mouth of Juan de Fuca Strait, and so could transport larvae out of the Puget Sound-Georgia Strait complex.

MATERIALS AND METHODS

General Methodology

Sampling was largely done along an offshore transect line perpendicular to the coast off Tofino, British Columbia (Fig. 1), with stations located at 0, 9.3, 18.5, 27.8, 37, 46, 55.6, 74.1, 92.3, 111.2, 148.2, and 185.3 km from shore. Stations were more closely spaced nearshore where larval abundance was expected to be greatest, but the transect extended well beyond the shelf break to determine what the seaward distribution of megalopae might be.

Six offshore samplings were made along the transect from February through August 1985, but only three extended the full 185 km. Dates of sampling were 27 February–4 March, 17 and 18 April, 30 and 31 May, 14 and 15 June, 6 and 7 July, and 24 and 25 August. February–March, June, and July samplings were terminated 74 km, 130 km, and 111 km offshore, respectively, because of poor weather and time constraints.

At each station, a neuston tow and an oblique bongo tow to 250 m, or to within 5 m of bottom, were made, and a temperature profile was recorded by means of an expendable bathythermograph. On all cruises, bongo tows were done during daylight hours and neuston tows at night; late-stage crab larvae congregate near the water surface at night (Booth et al. 1985). On 17 June 1985, an hourly, nocturnal series of neuston tows was made at one location, 9.3 km offshore, to identify patterns of nighttime abundance of megalopae in surface waters.

To supplement offshore sampling along the transect, neuston tows were made after dusk in the inlets around Tofino biweekly from early May through August 1985 to monitor presence and movement of larvae. In addition, a beam trawl and epibenthic sled were used in inshore waters in July 1985 to sample for newly settled larvae in an effort to establish time and magnitude of larval settlement.

The RV *G. B. Reed* was used for all offshore sampling except for the June sample, which was collected from a 27 m charter vessel. Inshore sampling was conducted from a 7 m aluminum herring skiff except for mid-June, when the charter vessel was again used.

Gear

The neuston sampler was a modified otter surface sampler (Mason and Phillips 1986) with a square mouth opening 45 cm on each side; under calm sea conditions, it sampled the top 35 cm of the water column. A General Oceanics flowmeter[3] in the mouth of the net was used to establish volume of water filtered. Netting was black, 500 μ Nitex, and

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

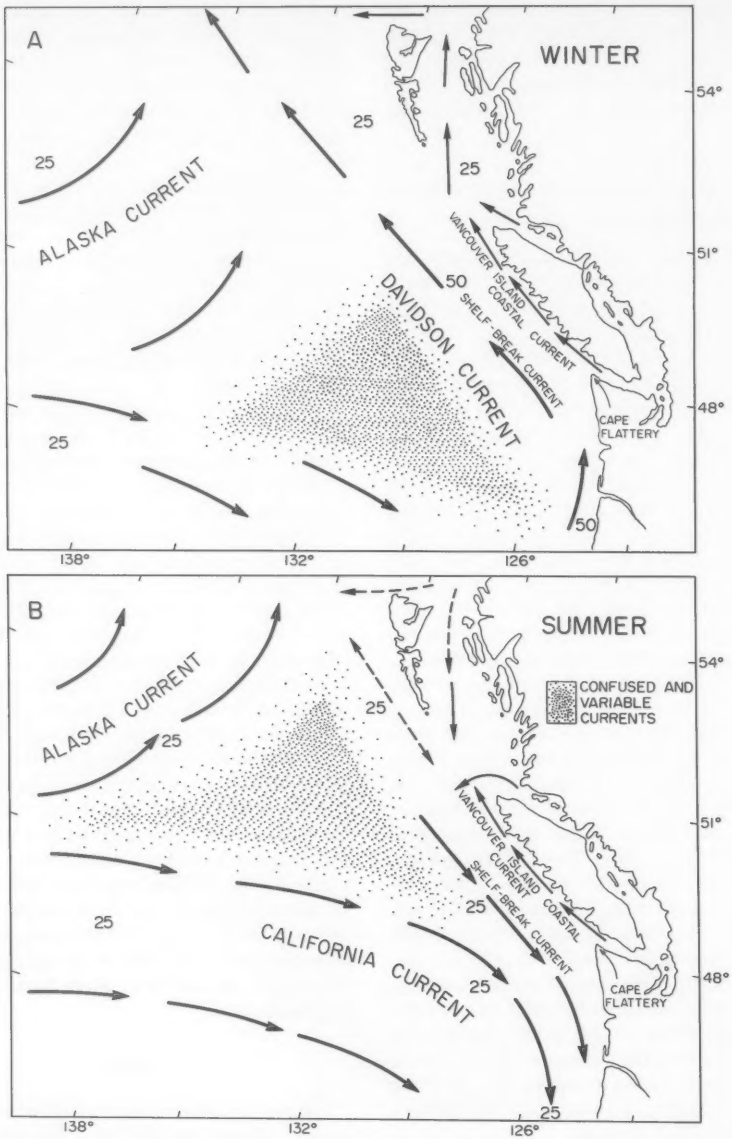


FIGURE 2.—Prevailing surface circulation off the British Columbia-Washington coast in winter and summer. Broken arrows indicate uncertain currents. Numbers give speeds (cm s^{-1}) (modified from Thomson 1981).

was the same size as that on the bongo gear. The neuston sampler was towed at 4 kn approximately 10 m from the side of the vessel to reduce hull avoidance by the larvae. Tow duration was usually 15 minutes but was shortened when crab larvae occasionally became very abundant at dawn and dusk.

Bongo gear was a modified SCOR design (Mason et al. 1984), having a mouth opening of 25 cm (each side) with the outboard (left) net of 500 μ Nitex and the inboard (right) net of 230 μ Nitex. A General Oceanics flowmeter was mounted in the mouth of each net. Sampling procedure followed that described by Smith and Richardson (1977[4]). At stations <100 m water depth, the bongo was fished in an undulating fashion from the bottom to the surface in order to filter a standard volume of water (about 300 m^3).

The epibenthic sled (Phillips and Mason 1986) used in inshore waters had a 60 cm mouth opening and 1 mm Nitex netting; it was towed for 10 minutes at 2–3 kn. Nine tows were made over bottoms of unknown characteristics. The modified beam trawl (Gunderson and Ellis 1986), also used in inshore waters, had a 3 m mouth opening, a 7 mm mesh net, and a 3 mm mesh cod end; it was towed for 10 minutes at about the same speed as the sled. For both gear types, distance towed was calculated by radar triangulation to reference points on land.

Data Analysis

All plankton samples were preserved initially in a 4% formaldehyde solution of saltwater. In the laboratory, settled volume was determined, and general composition of the plankton noted. Samples were then sieved, and *Cancer* larvae picked by hand and returned to a 2% formaldehyde solution before their identification. *Cancer magister* megalops are readily identifiable by their larger size (Trask 1970; Lough 1975), but the currently used key (Lough 1975) was not always effective in separating *C. oregonensis* and *C. productus*. Presence of lateral spines is a subjective criterion, and morphological dimensions and counts of setae were two variable to distinguish species. These smaller megalops were finally concluded to be *C. oregonensis* after rearing hundreds of larvae to the juvenile stage and finding no *C. productus*.

With beam trawl samples, the catch was sorted on deck to remove juvenile crabs, and the megalopae were preserved as above. Species composition of the catch was noted.

For the bongo tows, the volume of water filtered was used to calculate a haul factor (Mason et al. 1984), which accounted for tow depth and allowed expression of the data as the integrated number of organisms beneath 10 m^2 of sea surface.

For neuston tows, relative abundance was expressed as area swept rather than as volume filtered and again expressed as number of animals under 10 m^2 of sea surface.

Calculations of larval abundance are necessarily conservative, and direct comparisons between different gear types are not presently possible, given our current understanding of gear efficiency and larval catchability, which varies with both depth and time of day. Numbers of larvae reported here are thus directly comparable only within each gear type used. For bottom gear, numbers of crabs were calculated with no consideration of gear efficiency.

Molt Staging

State of development within the megalopal stage was determined for all *Cancer* megalopae collected at a station, or 25 randomly selected individuals of each species if the number collected exceeded 25. The sequence of epidermal changes occurring during this intermolt period has been described for Dungeness crab by Hatfield (1983), and her procedures and staging criteria were applied for both species. Whole megalopae were stained with 0.25% Fast Green dye in either water or polyvinyl lactophenol for 2–18 hours, and then the second maxillipeds were removed and mounted. Megalopae were identified to 1 of the 13 intermolt stages recognized by Hatfield (1983); these were then combined to form 3 groups: early (stages 1–4), middle (stages 5–8), and late (stages 9–13) megalopae. Temporal durations of these three groups in laboratory studies were 5.8, 15.4, and 6.3 days, respectively (Hatfield 1983). Corresponding durations for *C. oregonensis* are unknown. Stages were grouped into the three categories described for simplification of analysis; many of Hatfield's stages were of <48-h duration, and this was considered too fine a resolution for our purposes.

RESULTS

Water Temperature

Water temperature at the surface ranged from

[4]Smith, P. R., and S. L. Richardson. 1977. Manual of methods for fisheries resource survey and appraisal. Part 4. Standard techniques for pelagic fish egg and larval surveys. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Adm. Rep. No. 77-11.

8.4° to 14.4°C, and from 7.6° to 8.8°C at 50 m, during the period 17 April to 7 July (Table 1). Warmest surface temperatures were in May and July, and at 50 m, were warmest in June.

Species Occurrence

Three species of crab larvae predominated in the plankton collected. The porcellanid crab, *Petrolisthes cinctipes*, predominated in waters within 8 km of shore, while *C. oregonensis* and *C. magister* dominated in more offshore waters. Other crab species were present but at much lower abundance than these three species. Megalopae of *C. oregonensis* were of comparable abundance to *C. magister* at most stations sampled.

Surface Abundance

Presence of crab megalopae at the surface was dependent on time of day, with slight differences in timing of maximal abundance occurring between the two *Cancer* species (Fig. 3). At 9.3 km offshore in June, *C. oregonensis* was several orders of magnitude more abundant and also seemed to peak in abundance a little earlier in the evening and later in the morning than did *C. magister*. Relative abundance of both species declined in the middle of the night.

Data in Figure 3 was smoothed by eye (Fig. 4) to allow megalopal abundance data from the transect to be weighted by time of capture at night. Multiplier values were determined, and these were used to adjust actual abundance data by sampling time for the May and June sampling periods (Tables 2, 3). Only these data were weighted, and since day length changes with time of year, adjustment of data collected more than two weeks on either side of 14 and 15 June was considered inappropriate.

In hindsight, some data (indicated by asterisks in Tables 2, 3) was found to have been collected at a time when megalopae were just beginning to reach, or had just left, the surface. The calibration slope (Fig. 4) is very steep at both these times and it was impossible to estimate accurately a meaningful scaling multiplier for these data. Our estimated megalopal abundance at these stations should be viewed with particular caution; a zero value may not indicate that megalopae were absent, but only that they were not at the surface.

Bongo tows during the day poorly sampled the abundance of *C. magister* megalopae (Table 4) shown to be present by nighttime neuston tows (Tables 2, 3). This was possibly due to sampling the total column below only a few square meters of sea surface, because of integration of the results, or to avoiding the net by the megalopae. It was unlikely because of failure to sample deeply enough, since on the continental shelf, tow depth approached bottom depth. Megalopae (maximum per tow was 4) were primarily collected by bongo gear at stations where they were abundant in neuston samples at night, but relative abundance estimates obtained from bongo nets are considered only useful in a general qualitative sense because of the low absolute numbers caught.

Temporal Occurrence (Time of Year)

No *Cancer* megalopae were found in samples collected shortly after dusk on 27 February–4 March. *Cancer* megalopae were first observed on the next

TABLE 1.—Water temperatures (°C) by depth (m) at the stations sampled off Tofino, B.C. on 17 April, 31 May, 14 June, and 6 and 7 July 1985.

Distance offshore (km)	Depth (m)											
	April			May			June			July		
	0	20	50	0	20	50	0	20	50	0	20	50
0	8.8	8.8		12.2	9.2		12.2	11.4		—		
9	8.8	8.7		13.4	9.5		12.2	9.0		13.5	11.0	
19	8.7	8.1	7.9	13.4	8.6	7.6	12.3	10.4	8.0	14.0	9.0	7.6
28	8.8	8.8	8.2	13.1	9.6	7.9	12.8	12.3	8.0	13.3	10.0	7.7
37	8.6	8.6	8.3	13.8	9.3	7.9	12.7	9.4	8.3	13.3	10.7	7.7
56	8.7	8.7	8.2	13.3	9.8	8.2	12.9	10.5	8.1	14.4	13.3	8.6
74	8.7	8.6	8.2	11.8	10.0	8.2	12.9	12.0	8.7	14.4	13.3	8.6
93	8.5	8.5	8.2	11.9	10.3	8.2	12.8	12.2	8.5	—	—	
111	8.5	8.4	8.0	11.5	10.5	8.1	12.7	12.2	8.5	—	—	
130	—	—	—	—	—		12.7	12.4	8.6	—	—	
148	8.5	8.5	8.0	11.0	10.0	8.7	—	—	—	—	—	
185	8.4	8.6	8.4	11.4	10.0	8.4	—	—	—	—	—	

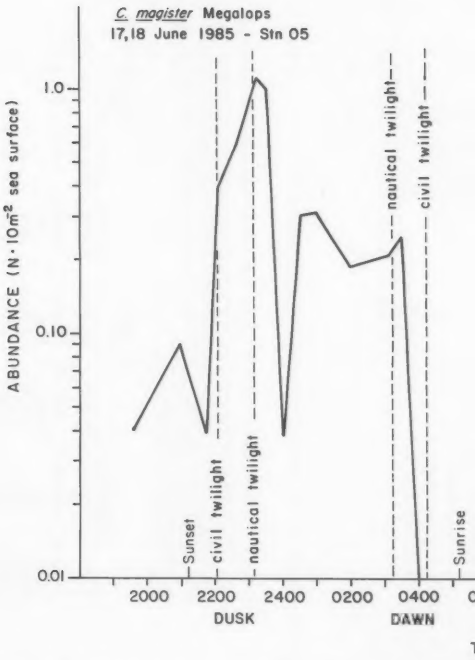
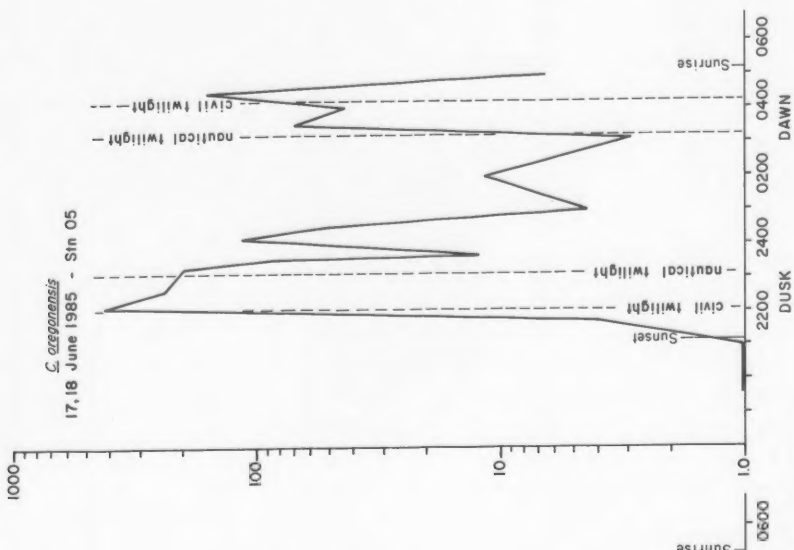


FIGURE 3.—Neustonic abundance of *Cancer magister* and *C. orego*
9 km off the



C. oregonensis megalopae observed during sampling through one night at a station off the coast off Tofino, B.C.

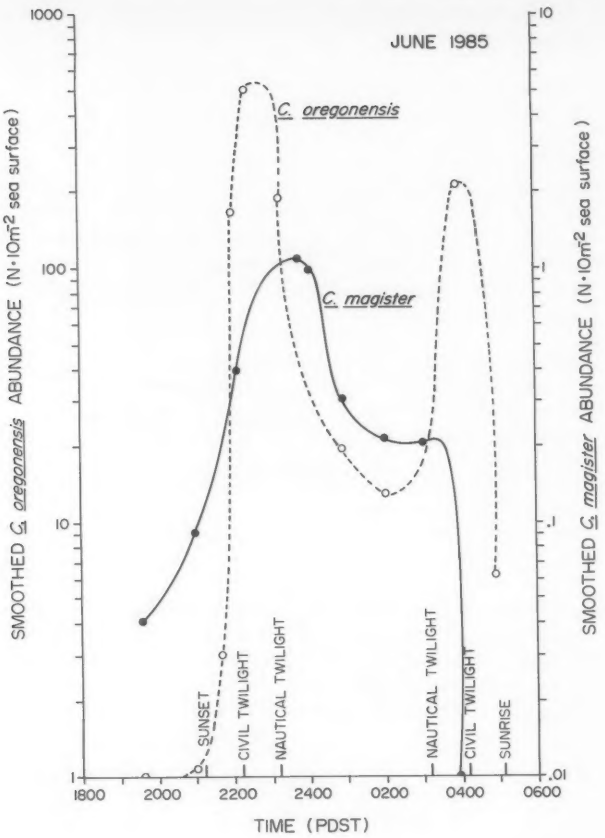


FIGURE 4.—Smoothed abundance of *Cancer magister* and *C. oregonensis* megalopae observed during sampling through one night at a station 9 km off the coast off Tofino, B.C.

TABLE 2.—Scaling values used to standardize the actual number of megalopae caught (unscaled) to the estimated number which would have been caught at the times of peak nocturnal abundance, 22:40 and 23:40 hours, for *Cancer oregonensis* and *C. magister*, respectively, on 30 and 31 May 1985. * = Value uncertain because of time of sampling. Values rounded to one decimal place.

Time	Distance (km)	*C. magister* (N 10 m^{-2})			*C. oregonensis* (N 10 m^{-2})		
		Multiplier	Unscaled	Scaled	Multiplier	Unscaled	Scaled
18:12	0	∞	2.3	?*	∞	0	0*
19:02	9	36.7	0.2	7.2*	∞	4	?*
19:43	19	26.8	0.0	1.1*	∞	0	0*
20:26	28	20.0	0	0	∞	0	0*
21:09	37	11.0	0.4	4.7	∞	0	0*
21:52	46	3.9	14.4	56.4	5.2	2.2	11.5
22:35	56	1.6	29.9	47.0	1.0	0.1	0.1
23:37	74	1.0	17.0	17.0	—	0	0
00:47	93	3.3	36.0	119.9	24.8	1.0	25.7
01:55	111	5.0	2.6	13.3	40.0	1.8	72.1
03:56	148	110.0	1.1	118.4*	2.5	0.1	0.2
05:57	185	∞	0	0*	∞	0	0*

sampling date, 16 and 17 April, but maximum abundance (unweighted as to diel time of sampling) occurred in late May and the second week of June (Fig. 5). *Cancer magister* megalopae were collected as late as 24 August, the last sampling date, but relative abundance along the transect was low after the beginning of July.

Cancer oregonensis megalopae were caught in April but occurred in abundance only in the late May and mid-June surveys, with peak abundance in June.

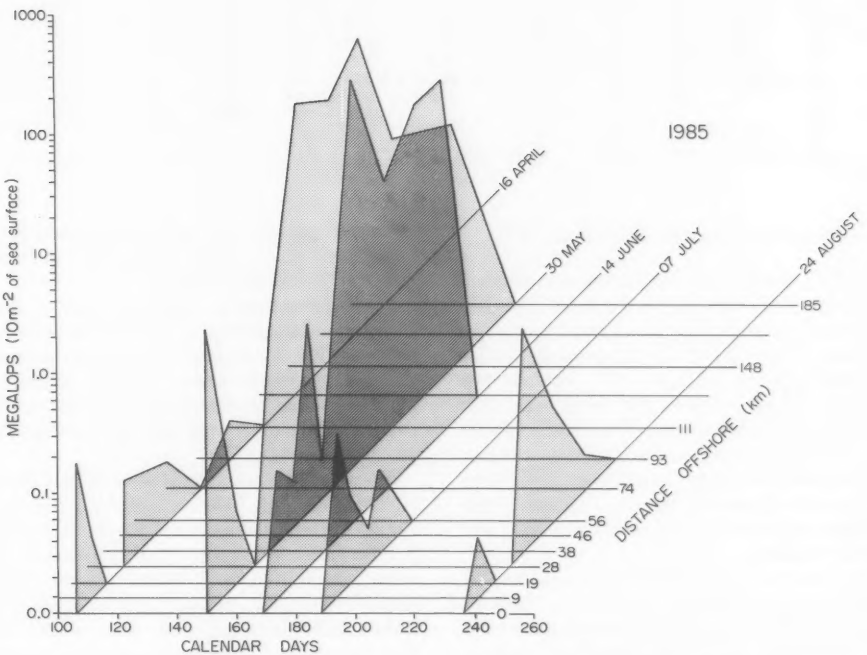


FIGURE 5.—Neustonic abundance of megalopae observed along the transect line during April to August 1985 surveys.

TABLE 3.—Scaling values used to standardize the actual number of megalopae caught (unscaled) to the estimated number which would have been caught at the times of peak nocturnal abundance, 22:40 and 23:40 hours, for *Cancer oregonensis* and *C. magister*, respectively, on 14 and 15 June 1985. * = Value uncertain because of time of sampling. Values rounded to one decimal place.

		C. magister (N 10 m^{-2})			*C. oregonensis* (N 10 m^{-2})		
Time	Distance (km)	Multiplier	Unscaled	Scaled	Multiplier	Unscaled	Scaled
01:42	0	—	0	0	37.1	8.8	327
00:58	9	3.6	0.1	0.4	27.4	170.5	4,671
00:09	19	1.2	0.1	0.1	16.3	0.1	2.3
23:19	28	1.0	0.2	0.2	2.7	7.6	20.5
05:36	37	∞	0.1	?*	∞	0	0*
03:52	56	55.0	52.2	2,871*	2.6	15.7	40.9
02:02	74	5.2	3.7	19.2	40.0	4.8	192
00:25	93	2.4	8.9	21.6	20.8	1.5	30.4
22:45	111	1.2	8.4	10.3	1.0	12.5	12.5
21:10	130	—	0	0	—	0	0

TABLE 4.—Tow characteristics and number of *Cancer magister* megalopae (10 m^{-2} of sea surface) caught by 0.25 m^2 bongo tows off Tofino, B.C., on 31 May and 14 June 1985.

	May					June				
Distance offshore (km)	Time (h)	Water volume (m^3)	Max. depth (m)	No. megalops	Megalopae (N 10 m^{-2})	Time (h)	Water volume (m^3)	Max. depth (m)	No. megalops	Megalopae (N 10 m^{-2})
0	19:27	210	33	1	1.6	08:00	240	36	3	4.5
9	18:52	182	55	1	3.0	08:55	220	55	0	0
19	18:16	114	72	0	0	09:51	222	75	0	0
28	17:37	166	120	0	0	10:50	209	115	0	0
37	16:55	199	151	0	0	11:47	284	146	1	5.1
56	15:30	352	250	4	28.4	13:32	381	192	0	0
74	14:07	327	250	1	7.6	15:21	338	200	1	5.9
93	12:42	326	250	3	23.0	17:04	296	200	2	13.5
111	11:17	360	250	1	6.9	18:56	269	200	0	0
130	—					21:12	327	200	2	12.2
148	08:55	400	250	0	0	—				
185	06:18	319	250	0	0	—				

Cross-Shelf Spatial Distribution

With both species, no clear pattern in cross-shelf distribution was evident from the April data, perhaps because of relatively low overall megalopal abundance. In late May (Table 2), scaled abundance (weighted as to time of night) of *C. magister* was highest at 93 km offshore, but megalopae were generally abundant (>10 10 m^{-2} sea surface) from 46 to 148 km offshore. In mid-June, the basic pattern observed in late May was still evident, although megalopal abundance near shore had declined (Table 3). Highest estimated *C. magister* abundance was at 56 km offshore.

With *C. oregonensis*, scaled abundance in late May peaked (>20 10 m^{-2}) 93–111 km offshore (Table 2). An exceptionally large number of megalopae (4,671 10 m^{-2}) was found 9 km offshore in June (Table 3), while from 56 to 111 km offshore, abundance remained high (>20 10 m^{-2}).

Sampling of inlet waters around Tofino with neuston gear showed that a few *Cancer* megalopae were present but that no substantial (average was <1 10 m^{-2}) numbers occurred. Maximum *C. magister* megalopal abundance was 2.9 megalopae 10 m^{-2} on 5 June, with megalopae observed only between 29 May and 19 June. Maximum *C. oregonensis* abundance was 2.3 megalopae 10 m^{-2} on June 19, with megalopae observed only between 4 and 19 June.

Intermolt Stage

All *C. magister* megalopae collected in April were of early developmental stage (Fig. 6), whereas all those collected in August were mid-stage megalopae. In May, June, and July, the general pattern of offshore distribution by molt stage was for late stage larvae to be nearest inshore and early stage larvae to be furthest offshore.

Cancer oregonensis megalopae had a similar developmental distribution pattern to those of *C. magister* (Fig. 7); late molt megalopae were most abundant closest to shore. However, in late May, most megalopae were early stage, in contrast to *C. magister*, whereas by mid-June, all three intermolt groups were present.

When the scaled megalopal abundance at distance offshore (Tables 2, 3) is multiplied by the percentage at each molt stage at a specific location (Figures 6, 7, for each species, respectively), the actual abundance by molt group with distance offshore is determined (Figures 8, 9, respectively). In late May, late stage *C. magister* megalopae were relatively abundant 9 km offshore, indicating that some Dungeness crab settlement may have occurred. However, larval sampling in the inlets and bays showed few megalopae present. In contrast to previous years, no recently settled juvenile crabs (0 age-class crabs) were found by local fishermen in intertidal areas or on floating objects, confirming that the magnitude of megalopal settlement in 1985 was relatively small. In mid-June, there were few *C. magister* megalopae of any intermolt stage present within 40 km of the coast and little evidence of late stage megalopae offshore. Early and mid-stage megalopae were most abundant from 56 to 111 km offshore.

For *C. oregonensis*, the opposite was observed (Fig. 9). Few late stage megalopae were present in late May, and unlike *C. magister*, megalopae were not concentrated in nearshore waters. However, megalopae in all three intermolt stages were abundant inshore in mid-June, with late stage megalopae dominating at the coast. The timing of occurrence

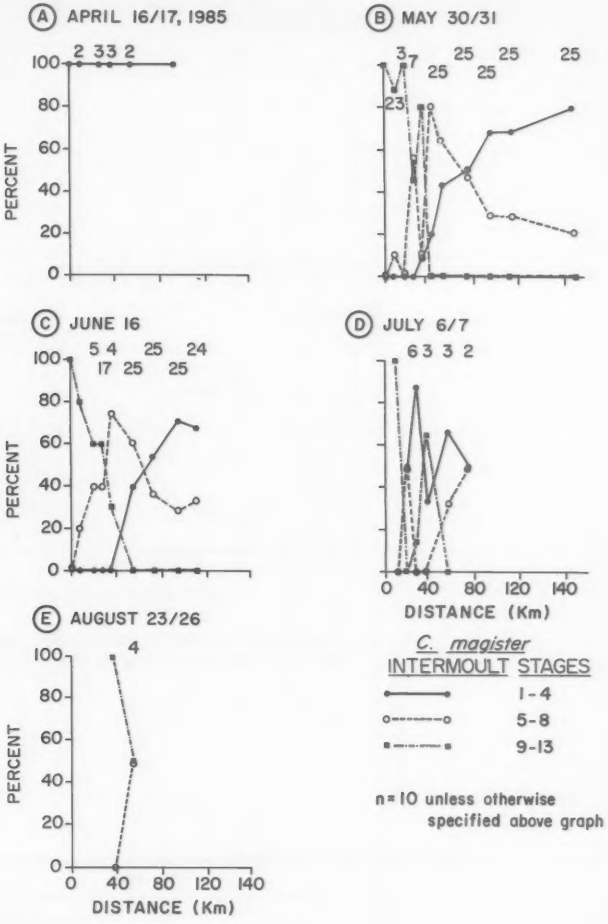


FIGURE 6.—Percentage of the three *Cancer magister* megalopal intermolt groups observed at each station during the April to August 1985 surveys.

of late stage megalopae at the coast thus differed between the two species.

Inshore Benthic Sampling

Survey of commercial crab habitat with beam trawls and an epibenthic sled yielded few newly settled megalopae or juvenile *C. magister* (Table 5). A maximum of 83 crab/10,000 m^2 was collected, well below densities which might be expected if settlement had been substantial. No *C. oregonensis* were caught, perhaps because of the habitat being sampled, and no larval settlement of either species was observed when intertidal mud flat areas were searched by foot. In a concurrent study, no significant abundance of 0 age-class *C. magister* was observed during monthly sampling throughout the remainder of the year.

DISCUSSION

Megalopal Source

Temporal duration of *C. magister* larval stages has been estimated both by laboratory rearing (Poole 1966; Reed 1969; Brugman 1972; Gaumer 1973; Ebert et al. 1983) and the first appearances of larval stages in field studies (Poole 1966; Lough 1976; Reilly 1983). The length of the total larval period has been estimated as 105–125 days by Reilly (1983),

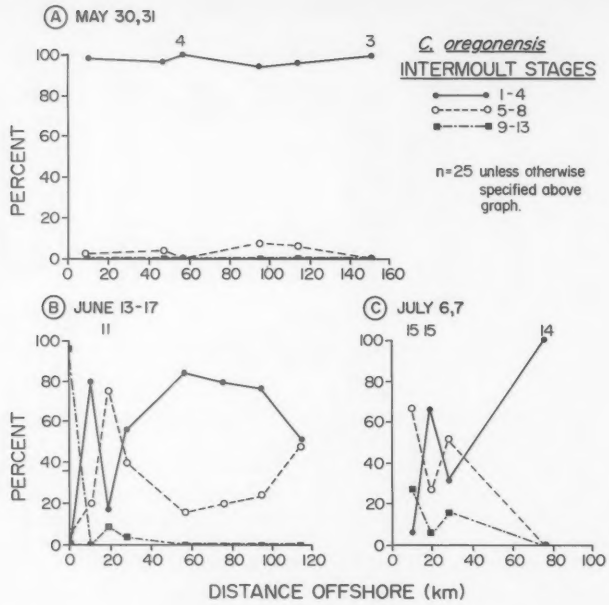


FIGURE 7.—Percentage of the three *Cancer oregonensis* megalopal intermolt groups observed at each station during the May to July 1985 surveys.

TABLE 5.—Beam trawl and epibenthic sled catches from nearshore waters around Tofino, 16–18 June 1985.

Area	Depth (m)	Gear type	Area swept (m^2)	Catch of crabs		No. 10^4 m^{-2}	
				Juveniles	Megalops	Juveniles	Megalops
Templar Channel	7	trawl	2,650	5	0	26	0
		sled	375	0	0	0	0
Chesterman Beach	5	trawl	—	—	—	—	—
		sled	300	0	0	0	0
Cox Bay	8	trawl	2,500	1	0	4	0
	7	sled	400	3	0	75	0
	13	trawl	2,600	7	0	27	0
	15	sled	420	2	0	48	0
	30	trawl	2,260	0	0	0	0
	23	sled	360	0	3	0	83
Lennard Island	25	trawl	—	—	—	—	—
		sled	350	0	0	0	0
Long Beach	7	trawl	2,700	5	0	18	0
		sled	400	2	0	50	0
	13	trawl	2,650	6	1	23	4
		sled	400	2	1	50	25
	23	trawl	—	—	—	—	—
		sled	220	0	1	0	45

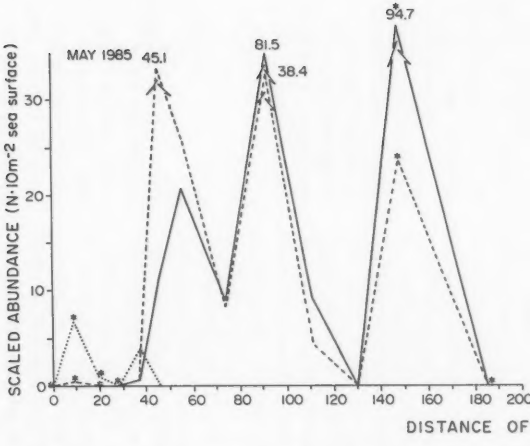
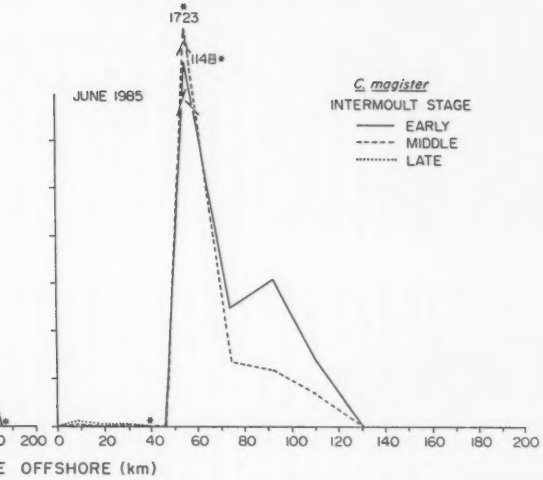


FIGURE 8.—Scaled abundance of *Cancer magister* megalopae by intermolt
* = Value uncertain becau



ermolt group observed at each station during the May and June 1985 surveys.
because of time of sampling.

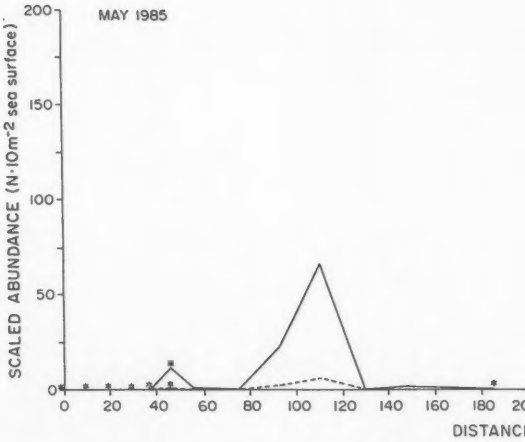
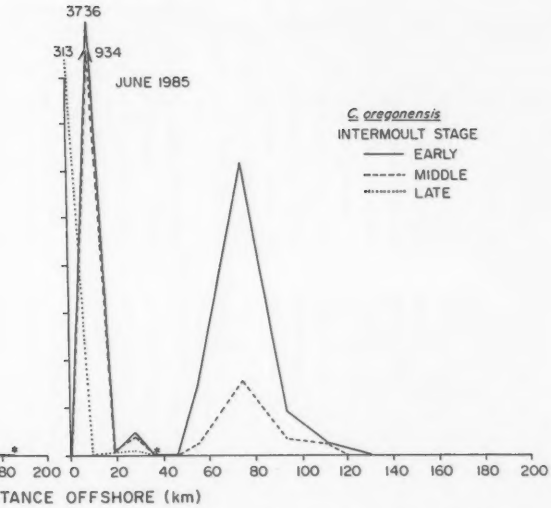


FIGURE 9.—Scaled abundance of *C. oregonensis* megalopae by intermolt
* = Value uncertain beca



ermolt group observed at each station during the May and June 1985 surveys.
n because of time of sampling.

130 days (range: 89–143) by Lough (1976), 45 and 108 days at 17.8° and 10.0°C, respectively, by Reed (1969), and 128–158 days under natural conditions by Poole (1966). In laboratory studies, Poole (1966) found the total time required was 111 days at 10.5°C. Since water temperatures typically range from about 8° to 13°C off the British Columbia-California coast during January-February (Thomson 1981), the total larval period in the study area is assumed to be about 110 days.

Off Vancouver Island, megalopae can be collected in abundance in open coast waters from mid-April to August. Ovigerous Dungeness crab, collected at Tofino and held in ambient temperature seawater at Nanaimo, hatched their eggs from January to March, with most hatching occurring in February (G. Jamieson, unpub. data). This suggests that megalopae collected between April and June could be from local populations whereas most megalopae collected in July and August may have largely originated elsewhere.

Lough (1975) stated that the hatching period of *C. oregonensis* off Oregon extends from January to July, with two broods indicated, one primarily hatching in February and the other in May–June. He estimated larval duration of a brood at 155 days (range: 123–203 days) from field sampling, but there was possible intermixing of the larvae from different broods, as well as population variability in the timing of hatching. We have no data on the hatching period of this species in British Columbia.

Given the currents off the west coast of Vancouver Island, then, *Cancer* larvae present there in the spring could theoretically have originated anywhere between northern California to perhaps southern Alaska. It seems very unlikely that the larvae are entirely the progeny of adult crabs on the west coast of Vancouver Island.

Onshore Movement

Geographical location of larval settlement is very dependent on currents. Adult *Cancer* of both species are largely found in nearshore, shallow-water habitats (Hart 1982), and such environments are apparently both the origin and preferred destination of larval crabs (Butler 1956). Along the open coast, Dungeness crab larvae are known to settle in both estuarine and nearshore areas (Wild and Tasto 1983; Stevens and Armstrong 1984; Armstrong and Gunderson 1985). In waters largely surrounded by land, such as Puget Sound, Georgia and Queen Charlotte Straits, and, to a lesser extent, Hecate Strait, Dixon Entrance, and southeastern Alaska, larval crabs may perhaps remain nearshore throughout their entire developmental period. However, studies suggest that while larvae may be hatched nearshore along the outer coast, they subsequently move offshore and then inshore (Lough 1976; Reilly 1983). The extent to which this may occur can profoundly affect the degree of dispersal of a local region's progeny.

Evidence for an offshore-onshore movement of *C. magister* during the larval development period is ambiguous. In the field, three studies of the offshore spatial pattern of larval distribution have been undertaken: off central and northern California (Reilly 1983), off Newport, Oregon (Lough 1976), and off Tofino, British Columbia (this study). The California study extended to about 185 km from shore from San Francisco north to Cape Mendocino, with some earlier CALCOFI data (1949–75) extending to about 275 km offshore included. Sampling consisted of discrete-depth and oblique plankton tows and was mostly during the day. The sampling gear (0.5 m diameter opening) most often used was preceded by the towing cable and bridle (P. Reilly[5]), and gear avoidence by same megalopae may have occurred. Because of the gear and protocol used, it is difficult to interpret Reilly's (1983) results in a quantitative sense. However, offshore movement of larvae during zoeal stages II–V was indicated, as was the later presence of megalopae in nearshore waters following a period when stage V zoeae were generally absent from within 40 km of shore, but a mechanism to explain the onshore transport of megalopae was not established. As part of the overall study (Wild and Tasto 1983), Hatfield (1983) determined the intermolt stage of many larvae collected by Reilly (1983). Earlier stage megalopae were in general collected further offshore, earlier in the year, and at a lower latitude.

The Oregon study (Lough 1976) was on one trackline extending 110 km offshore off Newport, with mostly daytime, oblique bongo samples collected at specified stations. Although early stage zoeae of both species were abundant nearshore, late stage zoeae were not, and were largely collected at the offshore stations. Lough (1975) noted that *C. oregonensis* megalopae were found further offshore and later during the summer upwelling season than were *C. magister* megalopae. In 1970, large numbers of *C. magister* megalopae, which were not intermolt staged, were found inshore. In 1971, virtually no *C. magister* larvae older than stage III were collected

[5]P. Reilly, California Department of Fish and Game, Menlo Park, CA 94025, pers. commun. February 1988.

at any of the stations, and Lough suggested that a mass mortality of *C. magister* larvae might have occurred. In contrast, *C. oregonensis* larvae were in greater abundance during 1971 than 1970.

Results from the current study and Booth et al. (1985) suggest that the sampling gear and procedures used by Reilly (1983) and Lough (1976) gave poor abundance estimates of megalopae. The number of megalopae caught during daylight is relatively low, and the presence or absence of only a few megalopae can greatly influence the estimated megalopal density per unit of sea surface. This sensitivity to bias can only be compensated for by many replicate samplings, and it is logistically easier to estimate absolute megalopal abundance by sampling at night when megalopae are concentrated in a relatively easily sampled, narrow depth range, namely the neuston (Booth et al. 1985). Reilly (1983) sampled once both day and night at 12 stations, and noted no significant differences in megalopal density between day and night at the surface and in oblique tows. However, his surface tows were not neuston tows, and consisted of a 0.5 m diameter net towed about 0.25–0.5 m below the water surface, or below the wave troughs if the surface was rough (P. Reilly fn. 5). This qualifies his observations, and may explain the suggested low abundance of megalopae in his study area (maximum density was 43 100 m^{-3} at the surface).

On occasion, megalopae have been observed to be in association with *Velella velella* at the surface during daylight (Wickham 1979; Reilly 1983; G. Jamieson unpub. data), but we have generally observed relatively few megalopae in surface waters during the day in comparison to the number observed present at night. Accepting that relative megalopal abundance is best determined at night from neuston tows, megalopae off British Columbia were shown to be abundant in specific areas offshore and at these locations, early and mid-stage megalopae predominated.

All three studies indicate that 1) later stage *C. magister* larvae are found offshore and, since they are hatched at inshore locations, some mechanism must be transporting them away from shore, 2) megalopae are found inshore, with Hatfield (1983) and this study showing that earlier stage megalopae predominate furthest offshore, and 3) while longshore drift of larvae may occur, it is difficult to establish its significance in the absence of simultaneous current and larval distribution data, both geographically and vertically in the water column. None of these studies demonstrates conclusively that larvae which ultimately settle inshore were ever very far offshore, and while it is shown that larvae can be carried offshore in abundance, this may well represent larval wastage, in that relatively few of them, if any, may ultimately return inshore to survive at settlement. The same is assumed to apply for *C. oregonensis*.

The California data on larval distribution, which is the most extensive spatially, are somewhat ambigious in that they may be interpreted either as onshore-offshore-onshore movement, or as a general offshore dispersal coupled with northwards-southwards drift of those larvae remaining inshore. To account for an absence of middle stage larvae in the nearshore waters of Reilly's (1983) study area, the latter scenario assumes that larval crab production south of the Gulf of the Farallones is relatively low, and that the water mass entering the sample area from the south as part of the Davidson Current contains few larvae. Little data appear to exist to refute this possibility; the commercial fishery for Dungeness crab only exists at a few locations south of San Francisco, and then only sporadically (Warner 1985). Our data and Lough's (1976) data are inadequate to investigate longshore drift because biological samples in each study were only collected along one offshore transect and no data on currents was simultaneously obtained.

Off the west coast of Vancouver Island, we found that megalopae may be concentrated in areas between surface currents flowing in opposite directions, specifically in the shear between the Vancouver Island Coastal Current and the outer Shelf-Break Current. Megalopae were abundant 40–70 km from shore, with *C. magister* megalopae particularly concentrated about 50 km from shore. In 1985, there was no major crab settlement observed on the outer coast near Tofino, suggesting that the Coastal Current may sometimes be an effective barrier to onshore movement and successful settlement. Understanding the horizontal and vertical distributions of crab larvae in the water column now seems essential if transport mechanisms of larvae and their movement from hatching to settlement are to be understood.

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FOOD PATHWAYS ASSOCIATED WITH PENAEID SHRIMPS IN A MANGROVE-FRINGED ESTUARY

ALLAN W. STONER[1] AND ROGER J. ZIMMERMAN[2]

ABSTRACT

High abundance and production of juvenile *Penaeus* spp. in tropical estuaries has been attributed to high concentrations of mangrove-derived detritus in the nursery habitats. Examination of the diets of *Penaeus notialis*, *P. subtilis*, and *P. brasiliensis* in the mangrove-fringed Laguna Joyuda, Puerto Rico showed that even the smallest juveniles are predators consuming capitellid polychaetes (20–38% of diets) and amphipods (20–76%). Less than 25% of the diets was detritus. Ontogenetic variation in diets was greater than interspecific variation, and there was no evidence for dietary separation among the sympatric species. Seasonal shifts in foods reflected abundance patterns of macrobenthic prey species. Despite the consumption of prey organisms generally classified as detritivorous, stable carbon isotope ratios in the penaeids (−18.1 to −15.0‰), their food items (−18.8 to −17.7‰), and primary producers indicated that shrimps and the majority of sediment dwellers in Laguna Joyuda obtain most of their carbon from benthic algae (−14.4‰) and not from mangrove detritus (−25.0 to −22.9‰).

The juveniles of penaeid shrimps are abundant in many tropical and subtropical estuaries of the world, particularly where wetland habitats such as marsh grasses or mangroves are prominent coastal features (Edwards 1978; Staples 1980; Stoner 1988). The relationship between wetlands and commercial shrimp has been attributed to at least two factors: high food abundance and shelter from predators, the relative importance of which is still debated (Boesch and Turner 1984). Early wetland studies (Odum and Heald 1972, 1975) suggested that a large variety of fishes and invertebrates including *Penaeus* spp. were directly dependent upon detritus from the vascular wetland plants. More specific studies of penaeid diets have since revealed that the shrimps are omnivorous or carnivorous in many shallow-water habitats (Moriarty 1976, 1977; Chong and Sasekumar 1981; Moriarty and Barclay 1981) and that some species may have a direct influence on the abundance of small macrofauna (Leber 1983, 1985).

The most important commercial shrimp species in the Caribbean Sea and along the north coast of South America are *Penaeus notialis*, *P. subtilis*, *P. brasiliensis*, and *P. schmitti*, all of which have nurseries in coastal wetland habitats (Stoner 1988). Although the biology of tropical Atlantic penaeids has been studied in a few localities (Neiva 1969; Nikolic and Ruiz 1969; Lindner 1971; Garcia 1974; Garcia et al. 1985), we have found no information on their diets.

Examinations of shrimp diets reported here were conducted in a small coastal lagoon in Puerto Rico where *Penaeus* populations are large and where four species coexist (Stoner 1988). In this report, diets of the three most abundant *Penaeus* species are described with particular reference to ontogenetic variation, similarities among the species, the significance of detritus, and seasonality in diets as related to the abundance of foods in the field.

Because foods are retained and assimilated differentially in the gut, examination of gut contents does not necessarily give a true indication of the relative importance of foods. For example, detritus has been reported as a significant component of the gut contents of *Penaeus* spp. (Odum and Heald 1972), but detritus is known to be indigestible compared with soft-bodied prey organisms such as polychaetes. Furthermore, in the case of predators, the primary source of carbon is not revealed through gut analysis. For these reasons, stable carbon isotope ratios were measured for *Penaeus* spp. and most other organisms common in the lagoon.

METHODS AND MATERIALS

Shrimps were collected in Laguna Joyuda on the west coast of Puerto Rico (lat. 18°07'N, long.

[1]Center for Energy and Environment Research, University of Puerto Rico, Mayaguez, Puerto Rico 00708; present address: Caribbean Marine Research Center, 100 E. 17th Street, Riviera Beach, FL 33404 and Lee Stocking Island, Exuma Cays, Bahamas.

[2]Southeast Fisheries Center Galveston Laboratory, National Marine Fisheries Service, NOAA, 2700 Avenue U, Galveston, TX 77550.

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67°11'W). The study site and shrimp and fish populations in the lagoon have been described by Stoner (1986, 1988). Briefly, Laguna Joyuda is a polyhaline basin with a total surface area of 1.21 km^2 and an average depth of approximately 1.5 m. One narrow channel 0.5 km long represents the only connection to the Puerto Rico shelf. Lagoon sediments are mostly fine mud and sand with very high organic content derived from red, white, and black mangroves which surround approximately 75% of the shoreline. Over the last 20 years the lagoon has had a salinity range of 4 to 44‰, depending upon precipitation and degree of channel closure (A. W. Stoner, unpubl. data).

Four penaeids utilize the lagoon as a nursery area. *Penaeus notialis* and *P. subtilis* are approximately equal in abundance and together comprise over 92% of the total penaeid assemblage (Stoner 1988). *Penaeus brasiliensis* made up 7.0% of the total collection in 1984 to 1985, and *P. schmitti* was relatively uncommon, making up <0.3% of the total (Table 1). For this study, we examined the diets of the three most abundant shrimp species.

Penaeids were collected with a 5 m otter trawl with 2.5 cm wings and body, and 5 mm cod end liner. All collections were made between nautical twilight and midnight at three sites: a northern muddy bottom arm of the lagoon (station 5), a sandy mud site in the central basin (station 3), and a sandy mud site near the channel (station 1). Collections were made monthly, during the last quarter of the moon, from July 1985 to June 1986.

Shrimps were divided into size classes on the basis of carapace length (CL) for gut content analyses. Penaeid shrimps between 3 and 6 mm CL could not be identified to species and were simply identified as *Penaeus* juveniles (all were of the grooved variety and, therefore, did not include *P. schmitti*). Shrimps larger than 6 mm CL could be identified and were examined by individual species in 4 mm size classes, up to 26 mm CL in the case of *P. subtilis*. To yield sufficient numbers of individuals in all size classes for each monthly collection, members of individual species were pooled from all sampling areas. In the case of *P. brasiliensis*, collections from 2-mo intervals were pooled to analyze seasonal variation in the diets of this less abundant species. Food items taken from the proventriculus of up to 25 shrimp were pooled for each sampling date and size class, and preserved with 70% isopropanol and a dilute solution of rose bengal stain.

We used the gravimetric sieve fractionation procedure developed by Carr and Adams (1972) to analyze gut contents of the shrimp. This procedure has been widely used for juvenile fishes (Sheridan 1979; Stoner 1980; Livingston 1984) and a variety of decapod crustaceans, including *Penaeus* spp. (Laughlin 1982; Leber 1983). Gut contents were washed through a series of six sieves of decreasing mesh size (2.0–0.075 mm mesh) and each sieve fraction was examined with a dissecting microscope. Because all of the items in a particular sieve fraction were of approximately equal size, the relative proportion of the gut contents made up of each food type was measured directly by counting. After examination, each sieve fraction was dried overnight at 80°C and the total contribution of each food type to total dry weight was calculated.

With few exceptions, each food particle was placed in a mutually exclusive category (Table 2). In most cases, food items or fragments could be identified to major taxonomic group such as Amphipod or Polychaete. The classification "Animal Remains" was applied where fragments were unidentifiable to taxon, but where the tissue was stained by rose bengal. The major food categories were used for statistical interpretation of diets; however, whenever an animal or plant could be identified to a lower taxonomic level, this information was recorded.

Similarities between and among the diets of various shrimp species and size classes were measured with Czekanowski's coefficient (Bray and Curtis 1957; Field and McFarlane 1968). Dendo-

TABLE 1.—Composition of the penaeid shrimp assemblage at three stations in Laguna Joyuda, Puerto Rico, during the 12-mo study period. Values are total numbers collected in 72 trawl samples and percentages of totals at the individual sites (parentheses).

Species	Station 1	Station 2	Station 3
Penaeus notialis	282 (49.1)	271 (53.6)	229 (48.6)
P. subtilis	236 (41.1)	185 (36.5)	217 (46.1)
P. brasiliensis	54 (9.4)	50 (9.9)	22 (4.7)
P. schmitti	2 (0.4)	0 (0)	3 (0.6)
Totals	574	506	471

TABLE 2.—List of the general food categories encountered in the foreguts of *Penaeus* species and the codes employed in histograms for shrimp diets.

AM	Amphipod	OS	Ostracod
CC	Calanoid copepod	PM	Plant material (green)
CY	Cyclopoid copepod	PO	Polychaete
CZ	Crab zoea	RU	*Ruppia maritimia*
DE	Detritus	SA	Sand
FO	Foraminifera	TA	Tanaidacean
FR	Fish remains	TH	*Thalassia testudinum*
HC	Harpacticoid copepod		
GA	Gastropod	MS	Miscellaneous—used in histograms for all food items making up <4% of the total dry weight.
IE	Invertebrate egg		
NE	Nematode		

grams were then constructed by complete linkage classification.

Plant and animal materials were collected from the lagoon for stable carbon isotope analyses on several occasions between 1981 and 1984. These were taken to give an indication of the range of $\delta^{13}C$ values between organisms associated with mangroves, plankton, and benthos and to test the efficiency of using the technique to identify food pathways. Materials were collected with trawl, sieve, plankton net, and by hand. All materials were fresh and not exposed to chemical preservatives. In the field, samples were placed in plastic bags on ice as temporary storage. Within 24 hours, these samples were flushed free of salt using deionized water, dissected to acquire tissue uncontaminated by gut contents and outside shells, treated for 5 to 10 minutes with 5% phosphoric acid to remove carbonates, double rinsed in deionized water, and oven-dried at 70°C until brittle. Dried samples were ground to a fine powder with a mortar and pestle, packaged in plastic bags, labeled, and stored for later mass spectrometer analyses. The homogenized samples were combusted at 550°C for 24 hours in the presence of CuO in evacuated sealed pyrex tubes using techniques modified from Stofer (1980). CO_2 gas was analyzed from the combusted samples on a Finnigan - MAT 251[3] isotope ratio mass spectrometer. $\delta^{13}C$ was calculated according to Craig (1957) and methods and definitions generally followed those reviewed by Fry and Sherr (1984). For small animals and all plants, the entire organism (with guts removed where possible) was used in analyses. For large animals, muscle tissue was removed from the body and used separately for analyses. In most cases, organisms were pooled to acquire mean $\delta^{13}C$ values for n individuals. Unlike more complex marine systems (Fry et al. 1982), our $\delta^{13}C$ were well separated between groups of species and distinctions were relatively clear-cut. Since diversity was also relatively low in the lagoon, $\delta^{13}C$ signatures in food pathways based on the dominant primary producers were easily detected. Some organisms with known restricted diets, that were closely associated with particular plants in the system, were selected as controls to follow trophic fractionation of $\delta^{13}C$. These included *Uca vocator* from the intertidal forest floor (a mangrove detritus feeder), *Haminoea antillarum* from the middle of the lagoon (an algae grazer), and *Balanus eburneus* and *Isognomon alatus* (filter feeders). Based on results of Fry et al. (1984), we assumed that ^{13}C enriched the isotope ratio by about 1‰ from one trophic level to the next.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

The Shrimp Community

The shrimp community composition during the study period was similar at the three sampling sites, except that *Penaeus schmitti* were not collected at station 3 (Table 1). *Penaeus notialis* dominated the shrimp assemblage in the lagoon (50.4%), followed by *P. subtilis* (41.1%), and *P. brasiliensis* (8.1%). Only five individuals of *P. schmitti* (0.3%) were collected in 12 months of sampling. Catch per unit effort over time was highly variable for each of the three primary species, with no distinct seasonality (Fig. 1). *Penaeus subtilis*, however, showed a general increase in abundance over the sampling period. *Penaeus brasiliensis* populations remained relatively low and stable throughout the year examined. Population and community structure of the penaeids in Laguna Joyuda has been examined in detail elsewhere (Stoner 1988) and the important point to be made here is that the three most abundant *Penaeus* spp. in Laguna Joyuda are sympatric in both time and space.

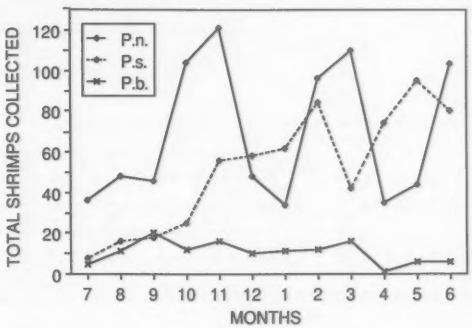

FIGURE 1.—Abundance of the three dominant *Penaeus* species in Laguna Joyuda, Puerto Rico, during the study period. The unit of effort for each sampling date is 18 trawl samples, pooled over all three stations. P.n. = *Penaeus notialis*; P.s. = *P. subtilis*; P.b. = *P. brasiliensis*.

Shrimp Diets

Over 1,300 *Penaeus* guts were examined for the present study. The proventriculi of most individuals contained freshly consumed food items; 89% of all

P. notialis, 87% of all *P. subtilis*, and 78% of all *P. brasiliensis* contained food. At least 50% of all animals in any one size class contained food on a given sampling date, but no seasonal or ontogenetic pattern in empty guts was evident.

The primary dietary components of all three penaeids were amphipods, polychaetes, harpacticoid copepods, and detritus (Fig. 2). For all species increase in shrimp size was correlated with decrease in the relative importance of harpacticoid copepods in the guts. Other small taxa such as nematodes and foraminifera also decreased with shrimp size. Detrital components of the diets remained relatively constant at approximately 20 to 25% of the gut contents. Abundance of polychaetes and amphipods changed relatively little with size in *P. notialis* and *P. subtilis*, except that amphipods increased in importance with size in *P. subtilis* and large quantities of amphipods were taken by the largest size class. Cluster analyses for the diets of individual species revealed little ontogenetic variation for these two species, except with the distinct separation of the largest *P. subtilis* (Fig. 2). For both *P. notialis* and *P. subtilis*, all size classes between 7 and 22 mm CL were clustered within similarity indices of 0.78. Although only three size classes were represented for *P. brasiliensis*, ontogenetic variation in *P. brasiliensis* was greater than in the other two species (Fig. 2). Polychaete consumption decreased from 47% of the diet in the 7 to 10 mm class to 22% in the 15 to 18 mm class, while amphipod consumption increased from 0 to 61%. Detritus consumption also decreased with size in *P. brasiliensis*, contributing to the low similarity indices among the size classes.

Four major clusters of shrimp feeding types were

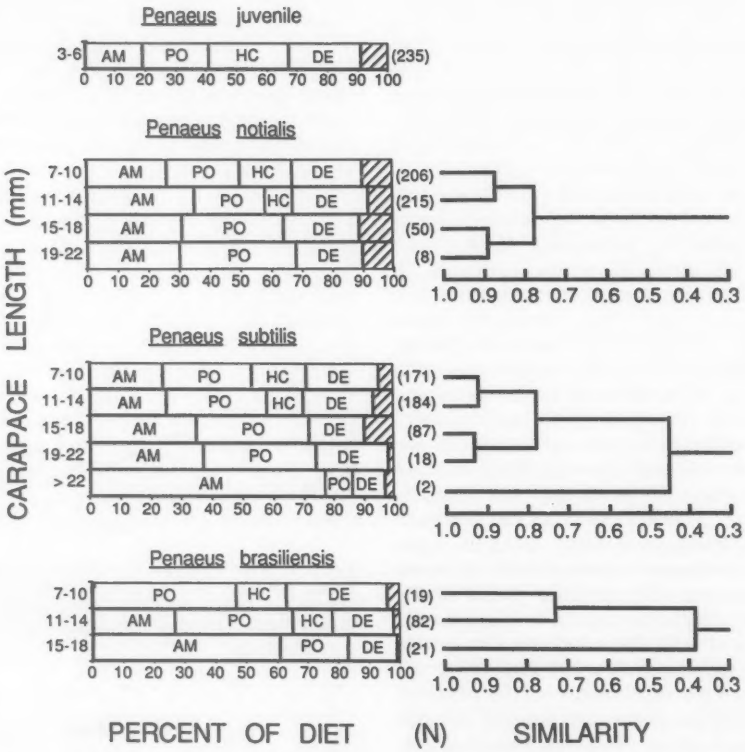

FIGURE 2.—Diets of the three dominant *Penaeus* species in Laguna Joyuda, Puerto Rico, shown as a function of shrimp size. Food categories are identified in Table 2. The similarity index used in the cluster diagrams is Czekanowski's coefficient.

revealed when the full matrix of similarity indices, including all species and size classes, was incorporated into a cluster analysis (Fig. 3). The greater ontogenetic variation in diets of *P. brasiliensis* resulted in the three size classes for the species falling into three distinct clusters, while all four size classes of *P. notialis* were included under two clusters. The largest *P. subtilis* were clustered with the largest *P. brasiliensis*. Except for *P. brasiliensis*, all shrimps between 7 and 14 mm CL were found in one trophic group and all between 15 and 22 mm CL were found in a second group.

Species or generic level identification of prey organisms indicated no species-specific differences among the diets of the three shrimp species. For all three species, all amphipods identifiable to species were *Grandidierella bonnieroides* and all identifiable polychaetes were nereids (probably *Nereis occidentalis* and *Steninonereis martini*). In *P. subtilis* and *P. brasiliensis*, all harpacticoid copepods were *Euterpina* spp. In *P. notialis*, 86% were *Euterpina* spp. and 14% were *Microsetella* sp. The calanoid copepods were a mixture of *Acartia tonsa* and *Pseudodiaptomus* spp.

Animals classified in groups 2 and 3 of the multispecies cluster (Fig. 3) contained sufficient numbers of individuals to make seasonal analyses of diets (Figs. 4, 5). Although harpacticoid copepods were taken in lower amounts by group 3 shrimps, by and large both groups showed similar seasonal trends in diet. Amphipods were taken in large numbers from July to October 1985 and from March through June 1986. Polychaetes and harpacticoid copepods were consumed most abundantly in November through March. Consumption of detritus was relatively constant in both groups, with slightly higher detrital intakes in group 2 individuals during November and December 1984.

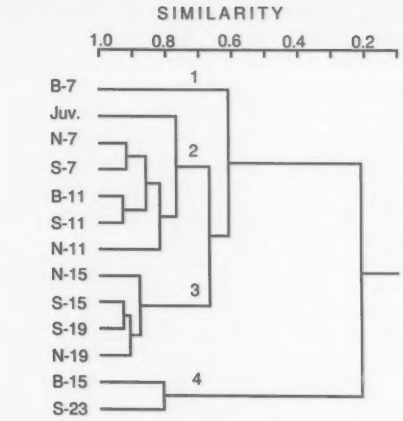

FIGURE 3.—Cluster diagram for the diets of shrimps incorporating all species and size classes. The cluster strategy is the same as that in Figure 2. Food categories are identified in Table 2.

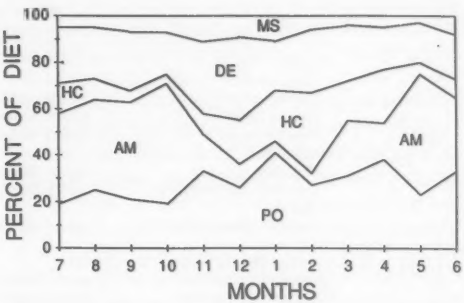

FIGURE 4.—Diets of shrimp trophic group 2 by sampling date.

Carbon Isotopes

The $\delta^{13}C$ values for three different samples of tissues from *Penaeus* spp. ranged from −15.0 to −18.1‰ (Table 3). These values were much higher than the plankton fraction <35 μ (comprised primarily of dinoflagellates; −26.8 to −27.2‰) or the primary copepod species in the lagoon, *Acartia tonsa* (−24.0 to −25.9‰). The $\delta^{13}C$ values for the shrimps are also much higher than the values for either mangrove leaves (green or dead), or detritus particles from the sediment, mostly of mangrove origin. The only primary producers with $\delta^{13}C$ values within the range of *Penaeus* spp. were the seagrass *Thalassia testudinum* (−16.1‰) and the

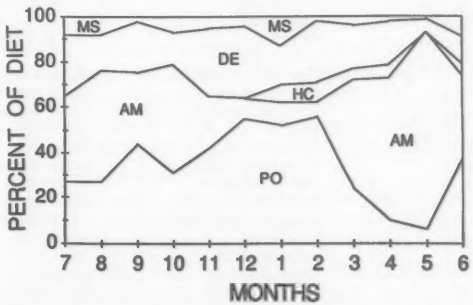

FIGURE 5.—Diets of shrimp trophic group 3 by sampling date.

algal mat comprised primarily of the filamentous blue-green alga *Spirulina* sp. Because there are only small patches of *T. testudinum* in Laguna Joyuda and the blue-green algae dominated the lagoon floor, the data suggest that the main source of carbon for penaeid shrimps in Laguna Joyuda is benthic blue-green algae. Blue-green algae also appear to be the primary source of carbon for other decapod crustaceans in the lagoon including *Callinectes* spp. and hermit crabs (Paguridae) (Table 3).

The carbon isotope data, suggesting algal sources of carbon for *Penaeus* spp., are consistent with the results of dietary analyses. The primary prey of penaeids were the amphipod *Grandidierella bonnieroides* and capitellid polychaetes. The $\delta^{13}C$ value for *G. bonnieroides* was within the range for *Penaeus* spp., −17.7‰. Similarly, when the bodies of capitellids were analyzed after removal of the guts, the $\delta^{13}C$ value of −18.8‰ also agrees with shrimps after adjusting for trophic fractionation of 1‰ less (Fry et al. 1984). Other organisms with $\delta^{13}C$ values similar to that of blue-green algae were the bubble snail *Haminoea antillarum* and the bivalve *Macoma brevifrons*. The carbon isotope ratios of these benthic feeders were more negative than *Spirulina* (−14.1‰), implying modification of $\delta^{13}C$ values from other sources; however, the major input appears to be from blue-green alga.

By contrast, organisms associated with the mangrove forest, *Uca vocator* (−23.0‰) and *Aratus pisonii* (−23.3‰), closely resembled carbon isotope ratios of detritus (−22.9 to −25.0‰). Moreover, the <35 μ plankton fraction (−26.8 to −27.0‰) and associated grazers, *Acartia* (−24.0 to −25.9‰), *Balanus* (−24.0‰), and *Isognomon* (−24.4‰), were not separable from the mangrove group. These data indicate that mangrove carbon is likely being incorporated into plankton-based food

TABLE 3.—Carbon isotope ratios in organisms associated with the penaeid shrimp food web in Laguna Joyuda, Puerto Rico.

Organisms	Tissue or composition	Number of pooled indiv.	Date of collection	$\delta^{13}C$
Plankton				
<35μ fraction		—	9/29/83	−26.8 to −27.2
Acartia tonsa	whole bodies	500	1/21/81	−25.9
Acartia tonsa	whole bodies	500	9/8/83	−25.2
Acartia tonsa	whole bodies	500	9/27/83	−24.0
Macroalgae				
Spirulina sp.	entire filaments	—	2/14/83	−14.2
Caulerpa sertularoides	entire alga	—	9/29/83	−20.2
Seagrass				
Thalassia testudinum	green leaves	—	9/29/83	−16.1
Mangroves				
Avicennia germinans	roots	—	2/14/84	−24.0
Rhizophora mangle	green leaves	—	9/24/81	−29.2
Rhizophora mangle	dead leaves	—	2/14/84	−27.3
Detritus				
Particules from the sediment		—	9/24/81	−22.9 to −25.0
Polychaetes				
Capitellidae	body without gut	13	9/24/81	−18.8
Capitellidae	whole bodies	10	2/14/81	−23.1
Capitellidae	whole bodies	10	9/30/81	−22.0
Capitellidae	whole bodies	10	2/14/84	−22.9
Nereidae	whole bodies	2	2/14/84	−21.6
Mollusca				
Haminoea antillarum	whole bodies	1	9/24/81	−15.8
Isognomon alatus	whole bodies	6	9/24/81	−24.4
Macoma brevifrons	whole bodies	6	9/24/81	−18.8
Crustacea				
Aratus pisonii	leg muscle	10	9/30/81	−23.3
Balanus eburneus	whole bodies	20	9/24/81	−24.0
Callinectes danae	claw muscle	2	2/14/84	−15.4
Callinectes sapidus	claw muscle	1	2/14/84	−16.4
Grandidierella bonnieroides	whole bodies	52	2/14/84	−17.7
Pagurus sp.	leg muscle	3	2/14/84	−16.2
Penaeus notialis	tail muscle	12	9/31/81	−18.1
Penaeus notialis	tail muscle	10	2/14/84	−15.4
Penaeus subtilis	tail muscle	10	2/14/84	−15.0
Petrolisthes sp.	whole bodies	12	9/24/81	−23.5
Uca vocator	leg muscle	10	9/30/81	−23.0

chains in the lagoon. This can be supported using *Acartia* as a link, since the copepod is known to feed on detritus particles and because the growth of *Acartia* is improved with detritus is included in the diet (Roman 1984). Suspended detritus particles from mangroves were a component of our <35 μ plankton fraction, suggesting availability to planktonic consumers.

DISCUSSION

Early studies of penaeid diets led to the general conclusion that the shrimps were largely detritivorous with incidental amounts of animal or plant material in the guts (Williams 1955; Darnell 1958; Odum and Heald 1972). Dall (1968) concluded that several Australian penaeids were not predators, but consumers of small-sized and disabled animals. Although penaeid shrimps are known to sort sediments for organic particles with their delicate pereiopods (Dall 1968; Lindner and Cook 1970) it is now apparent that penaeid shrimps are capable of taking prey organisms such as large polychaetes, as well as the more difficult prey such as gastropods and bivalves, caridean shrimps, crabs, echinoderms, and even fishes (Moriarty 1977; Marte 1980; Leber 1983). Lindner and Cook (1970) reported that *Penaeus setiferus* is cannibalistic at times. The relatively constant low amount of detrital particles in the guts of shrimp from Laguna Joyuda suggests that the less readily digestible detritus is taken incidentally with animal prey or as a response to low prey abundance. In addition, Gleason and Zimmerman (1984) showed that nematodes, oligochaetes, polychaetes, and copepods were stripped from detritus by *P. aztecus* during feeding. Reports of shrimp filled with unrecognizable debris assumed to be detritus may be a consequence of actual detritus consumption or incomplete development of methods sufficient to make animal remains identifiable.

Despite considerable attention given to feeding in the commercially significant penaeids, relatively few investigators have examined ontogenetic variation in diets. In this study, even within juvenile size classes, there were clear patterns of dietary change with shrimp size. All three of the subject species abandoned smaller prey organisms such as foraminifera, nematodes, and harpacticoid copepods in favor of amphipods, polychaetes, and shrimp as the predators became larger. Similar findings were reported by Leber (1983) for *P. duorarum*. These ontogenetic shifts in prey are undoubtedly related to increasing size of the chelae and mouth parts and must be considered in any ecological interpretation of trophic position; Moriarty (1977) suggested that the great opportunism of penaeid shrimps precluded their being placed in one trophic group throughout their life cycle.

On the other hand, with the exception of accelerated ontogenetic shifts in the diets of *P. brasiliensis*, interspecific variation in feeding in Laguna Joyuda were relatively minor. Despite high abundance and great temporal and spatial overlap in the *Penaeus* spp. of the lagoon (Stoner 1988), coupled with very low biomass values for macrofauna (<2 g dry wt/m^2), there is no evidence for resource partitioning among the grooved shrimps.

Seasonal diets in *Penaeus* spp. were coincident with seasonal trends in the abundance of major prey organisms. In the lagoon, the one important amphipod species, *Grandidierella bonnieroides*, demonstrated maxima between July and September and again from May to June; this corresponded with maximum amphipod consumption between July and October and March through June in the same year as benthic studies. Polychaete consumption was highest between November and March (particularly in the group 3 shrimps), corresponding with the October to April peak in capitellid abundance in the lagoon. Consequently, the oscillation in polychaete and amphipod feeding appears to be related to the availability of foods.

The hypothesis that mangrove estuaries are fueled primarily by carbon from mangrove detritus has become established from the pioneering work on mangrove-associated food webs conducted in the North River estuary of south Florida (Odum and Heald 1972, 1975). Mangrove litter inputs to Laguna Joyuda are high (Levine 1981), the sediments are rich in organic content, and detritus comprised a portion of the gut contents of juvenile shrimp. It is unlikely, however, that a large amount of carbon derived from detritus or detritus-associated microbes contributes in a large way to the tissues of the shrimp in the lagoon. In fact, the only organisms which had carbon isotope ratios similar to that of detritus were those normally found in direct association with the trees such as fiddler and mangrove crabs. The $\delta^{13}C$ values for shrimp in Laguna Joyuda were, in fact, very similar to values for penaeids from the open waters of the Gulf of Mexico (Fry and Parker 1979).

Benthic algal primary production in Laguna Joyuda is probably highly significant because carbon isotope ratios in the algae and shrimp were similar. Gleason (1986) also found that juvenile *P. aztecus* penaeids in a Galveston Bay salt marsh derived their carbon from blue-green algae, green

algae, and epiphytes of salt marsh grasses, not from *Spartina* detritus. Algal foods also proved to be the primary source of carbon for penaeids in Georgia marshes (Hughes and Sherr 1983) and in *P. duorarum* inhabiting seagrass beds in the Gulf of Mexico (Leber 1983) where food webs have long been considered detritus based. The significance of algal production in mangrove areas has been pointed out by Rodelli et al. (1984). They concluded that both mangrove and algal carbon were utilized by most of animals in a Malaysian swamp, but virtually no animals collected at distances >2 km from the swamp contained mangrove-derived carbon. To this date, there is little evidence to suggest that natant species such as fishes and decapod Crustacea can use detritus as a primary food source even if microbially enriched (Boesch and Turner 1984).

Localities where mangroves grow often support a variety of other primary producers, and variation in the relative significance of detrital and algal carbon sources may be associated with tidal amplitude and flushing. Laguna Joyuda, with microtidal influences, appears to be fueled by algal carbon whereas shrimp-producing mangrove areas in Ecuador have meso- and macrotidal regimes and no apparent algal growth (Zimmerman, pers. observ.). That mangroves provide critical substratum and protective cover for a large number of organisms is undisputed; however, the assumed significance of mangrove-derived detritus should be examined further.

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THE EFFECT OF THE ECTOPARASITIC PYRAMIDELLID SNAIL, *BOONEA IMPRESSA*, ON THE GROWTH AND HEALTH OF OYSTERS, *CRASSOSTREA VIRGINICA*, UNDER FIELD CONDITIONS

ELIZABETH A. WILSON,[1] ERIC N. POWELL,[1] AND SAMMY M. RAY[2]

ABSTRACT

Boonea (= *Odostomia*) *impressa* are contagiously distributed on oyster reefs so that some oysters are parasitized more than others. The parasite's mobility and the ability of oysters to recover from snail parasitism may be important in assessing the impact of parasitism on oyster populations. During a 4-week exposure period in the field, *B. impressa* reduced American oyster, *Crassostrea virginica*, growth rate and increased the intensity of infection by the protozoan, *Perkinsus* (= *Dermocystidium*) *marinus*, but produced few changes in the oyster's biochemical composition because, although net productivity was reduced, the oysters retained a net positive energy balance (assimilation > respiration). During a 4-week recovery period, growth rate returned to normal (control) levels, but infection by *P. marinus* continued to intensify in previously parasitized oysters kept *B. impressa*-free. Most changes in biochemical composition during recovery, including increased lipid and glycogen contents, could be attributed to the continuing increase in infection intensity of *P. marinus*. Consequently, the temporal stability and size of snail patches, particularly as they regulate infection by *P. marinus*, may be the most important factors influencing the impact of *B. impressa* on oyster reefs.

Parasitism can be an important factor affecting the population dynamics (Wickham 1986; Brown and Brown 1986; Kabat 1986) and health (Brockelman 1978; Mohamed and Ishak 1981; Ford 1986) of host species. Three parasites are known to be especially important in oysters. *Perkinsus* (= *Dermocystidium*) *marinus*, *Haplosporidium nelsoni* (MSX), and *Boonea* (= *Odostomia*) *impressa* detrimentally affect oyster growth, health, and biochemical composition (Mengebier and Wood 1969; Feng et al. 1970; Soniat and Koenig 1982; White et al. 1984; Ford 1986; Ward and Langdon 1986; White et al. 1988, in press).

The pyramidellid gastropod, *Boonea impressa*, is one of a widely distributed group of parasitic, marine opisthobranchs (Fretter and Graham 1949; Fretter 1951; Allen 1958). *Boonea impressa* removes nutrients directly from its host by piercing the flesh with a hollow stylet and sucking the body fluids using a buccal pump (Fretter and Graham 1949; Fretter 1951; Allen 1958). The most common host of *B. impressa* is *Crassostrea virginica* (Hopkins 1956; Allen 1958; Wells 1959) but, like other odostomians, it is not entirely host specific (Wells 1959; Robertson 1978; Robertson and Mau-Lastovicka 1979). Found abundantly on oyster reefs from Massachusetts to the Gulf of Mexico, *B. impressa* has been reported in numbers as high as 100 per oyster (Hopkins 1956).

Under laboratory conditions, *B. impressa* reduced oyster growth rates as the result of both direct removal of assimilated carbon from the oyster and direct interference with the oyster's ability to feed (White et al. 1984, 1988; Ward and Langdon 1986). Not surprisingly, parasitism by *B. impressa* produced changes in the biochemical composition of oyster tissue. Parasitism by 15 snails, a relatively high field density found in dense snail patches decreased carbohydrate and free amino acid content and increased lipid content of mantle tissue. Reproduction was affected as well (White et al. in press).

Perkinsus marinus is an important cause of mortality of oysters in the Gulf of Mexico (Mackin 1962; Ray 1966a; Hofstetter 1977). Sublethal effects include reduced growth (Menzel and Hopkins 1955; Ray et al. 1953) and changes in biochemical composition (Soniat and Koenig 1982; White et al. in press). *Perkinsus marinus* can be transmitted from one oyster to another through the water (Ray 1954; Mackin 1962; Andrews 1965) or by *B. impressa* feeding (White et al. 1987). The intensity of infection by *P. marinus* is also increased in *B. impressa*-parasitized oysters (White et al. 1987).

Usually stress affects organisms by altering normal metabolic activity. Many organisms may be able

[1]Department of Oceanography, Texas A&M University, College Station, TX 77843.
[2]Department of Marine Biology, Texas A&M University at Galveston, Galveston, TX 77550.

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to return to normal metabolic condition after the stress is removed (Pörtner et al. 1979; Pickering et al. 1982; Kendall et al. 1984). This ability, termed recovery, is an important adaptation to changes in the natural environment. Recovery is not always complete nor does it occur over relatively short time scales in all cases. The time required for recovery varies depending on the parameter being studied, the stress that was applied, and the species involved (Kendall et al. 1984; Haux et al. 1985; Neff et al. 1985). Apparently deleterious effects occurring after exposure, during the so-called recovery period, are well described (e.g. Kendall et al. 1984; Powell et al. 1984). White et al. (1984) showed that *C. virginica* could attain normal growth rates within one week after *B. impressa* were removed. However, growth rates frequently return to normal more rapidly than other metabolic parameters (Kendall et al. 1984). *Boonea impressa* are extremely mobile and are more contagiously distributed than their hosts, so that some oysters are highly parasitized while others remain parasite free (Powell et al. 1987). Individual *B. impressa* change hosts often but typically move between existing aggregates (Wilson et al. in press). Therefore, refugia from parasitism may exist and recovery may be important in assessing the overall impact of *B. impressa* on oysters.

Stress, produced by laboratory conditions, frequently accompanies laboratory experimentation (e.g., Koenig et al. 1981; Powell et al. 1984; Kukal and Kevan 1987). The effect of *B. impressa* on *C. virginica* has been assessed primarily through laboratory experimentation. Consequently, we examined the effect of *B. impressa* on *C. virginica* under field conditions and assessed the ability of oysters to recover normal growth rates and biochemical composition once snail parasitism ceased.

MATERIALS AND METHODS

Field Study

Oysters and snails used in this study were collected at Goose Island State Recreation Area near Rockport, TX. The oysters were weighed on a Mettler balance using the underwater method of Andrews (1961). Fifteen oysters (precontrols) were sacrificed to define the biochemical composition of the oysters and *Perkinsus marinus* levels that existed naturally at the collection site. The rest of the oysters were placed in semi-enclosed plexiglass domes (see figure 2 in Kendall et al. 1984 for description) in a tidal creek near the Aransas Pass Lighthouse on Lydia Ann Channel, near Port Aransas, TX. The domes allowed water to circulate over the oysters, while excluding such large predators as oyster drills and crabs. *Boonea impressa*, however, could readily move into or out of the domes.

Two of the four domes (20 oysters per dome) contained oysters exposed to *B. impressa* at a concentration of 10 snails per oyster, a level of parasitism commonly observed on reefs in the collection area (White et al. 1984). The domes were positioned so that the probability of snails moving from the exposure domes with parasitized oysters to the control domes was minimized (Fig. 1). Snails on each experimental oyster were counted twice weekly for 4 weeks. No *B. impressa* were ever found on control oysters. *Boonea impressa* did emigrate from the exposure domes, however, so snails were added as needed to maintain the 10:1, snail:oyster ratio. Control oysters were handled the same as experimentals each week in an effort to minimize differential effects caused by handling stress (see Pickering et al. 1982; Andrews and Hewatt [1957] were unable to find any effect of handling on *P. marinus* infection in oysters).

At the end of 4 weeks, the oysters were reweighed and half from each dome were sacrificed. The remaining oysters were replaced in the field for a 4-wk recovery period without *B. impressa*. All *B. impressa* were removed from the previously parasitized oysters by hand prior to replacement. The domes were visited twice weekly and each oyster handled as before. No *B. impressa* were found on the oysters during the recovery period.

Laboratory Analysis

Perkinsus marinus infection was measured in each oyster by incubating a small piece of mantle tissue in thioglycollate medium by the method of Ray (1966b). Intensity of infection was based on a semi-quantitative 0 to 5 rating assigned during microscopic inspection of the tissue after treatment with Lugol's solution (Mackin 1962). Small pieces of gonadal tissue were preserved in Bouin's fixative, sectioned and stained in 0.5% toluidine blue (Preece 1972) for gonadal analysis. Mantle cavity volume was determined by filling the shells with silicon caulking. Oyster growth, as expressed by shell deposition, was measured using the underwater weighing method. Condition index was derived by dividing the total lyophilized dry weight by the mantle cavity volume (Lawrence and Scott 1982).

The mantle and adductor muscle from each oyster

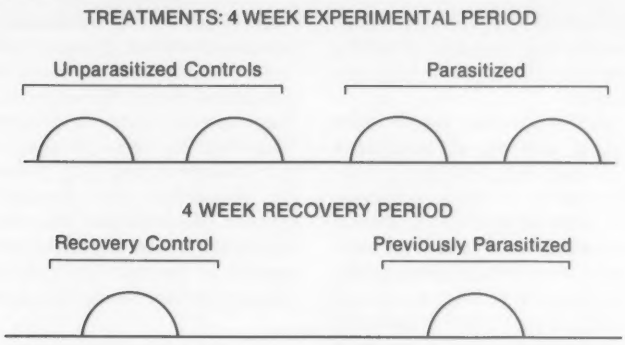

FIGURE 1.—Position of plexiglass domes during 4-wk experimental period and during 4-wk recovery period.

were frozen immediately on dry ice and kept at −40°C until lyophilized. Prior to biochemical analysis, lyophilized tissues were weighed and homogenized on ice. Total lipids were isolated from a portion of the homogenate using the water:methanol: chloroform method of Folch et al. (1957) with a modified ratio of 0.8:2.1. This isolation produced a two phase system and an insoluble pellet after centrifugation in the cold. The pellet was used for protein and glycogen assays. The water phase was used for amino acid analysis. The organic phase was divided and dried under N_2 gas at 40°C. One half was used to determine lipid phosphate concentration by the spectrophotometric method of White et al. (1979). The other half was dissolved in chloroform to which nonadecanoic acid was added as an internal standard. The redissolved lipids were fractionated on a silicic acid (Unisil,[3] 100–200 mesh) column. Neutral lipids were recovered by eluting with 10 times the column volume of chloroform. The chloroform was removed under N_2 at 40°C (Gehron and White 1982). The resulting chloroform fraction, containing fatty acid methyl esters, was analyzed by gas chromatography using a capillary, nonpolar, methyl silicone high performance column and flame ionization detector.

The amino acids were analyzed on a Dionex 3000 amino acid analyzer. Because residual chloroform interfered with the analysis, a second extraction was performed on the sample in the cold using a chloroform:water ratio of 1:3; α-amino-n-butyric acid (2.5 μmole $\cdot$ mL^{-1} sample) was used as an internal standard. The amino acids accounting for the bulk of the free amino acid (FAA) pool, taurine, hypotaurine, aspartic acid, serine, threonine, glutamine, glutamate, glycine, and alanine, were separated using a lithium citrate buffer and measured using o-phthalaldehyde as the detecting compound.

Total soluble protein was estimated by Peterson's (1977) modification of the Lowry method. Protein was precipitated using a final concentration of 10% trichloroacetic acid in the cold. After centrifugation at 4°C the resultant pellets were resuspended in 50:50, 10% SDS:0.8N NaOH for 30 minutes. Replicate samples were centrifuged and analyzed spectrophotometrically for protein concentration. Bovine serum albumin (Sigma) was used as the standard.

Glycogen was degraded to glucose enzymatically with amyloglucosidase (Carr and Neff 1984). After preincubation with amyloglucosidase, glucose was measured using the glucose oxidase-peroxidase procedure (Sigma glucose kit) (Roehrig and Allred 1974). Rat liver glycogen (Sigma) was used as a standard.

Statistical Analysis

To assess the effect of *Boonea impressa* on the oysters during the 4-wk exposure period, the level of snail parasitism for each oyster had to be determined. Because the number of snails on each oyster was counted only every third day, the total number of snails that parasitized each oyster was estimated by assuming that the same number of snails were present on days between counts as found on the previous visit. The total number of snail-days per oyster, the sum of the number of snails present on each day during the 4-wk exposure, will be referred to as the snail scale. For example, during the first week of the exposure period, one oyster had 15

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

snails on Monday, 10 on Wednesday, and 4 on Saturday; therefore Tuesday was assigned 15 snails, Thursday and Friday 10 snails, and the total for the week was 64 snail-days.

Except where noted in the text, results were analyzed by multiple analysis of covariance (MANCOVA) using ranked data followed by Duncan's multiple range tests ($\alpha = 0.05$) to locate significant differences within the MANCOVA. Mantle cavity volume was used as the covariate for comparing levels of *P. marinus* infection intensity, dry weight, and shell weight gain between treatment groups (e.g., parasitized and control oysters). Similar tests comparing biochemical parameters between treatment groups included the intensity of *P. marinus* infection and tissue dry weight as covariates. When the requirement of parallelism was not met, the MANCOVA was modified as described by Smith and Coull (1987). *Perkinsus marinus* infection intensity was used as both a dependent and independent variable because, although *B. impressa* can influence the intensity of *P. marinus* infection (White et al. 1987), *P. marinus* itself can affect the biochemical composition of oysters (Soniat and Koenig 1982; White et al. in press). Only parasitized oysters (or those recovering from parasitism) were used in analyses of the effect of snail scale (intensity of parasitism).

The FAA pool was analyzed three ways: 1) the entire pool, 2) the pool minus taurine and hypotaurine because these are the only amino acids not found in protein, and 3) after exclusion of the major components (taurine, hypotaurine, glycine, and alanine) so that changes in the lesser constituents of the pool could be examined.

All analyses for the 4-wk exposure period used MANCOVA analyses with nested variables, which took into account which of the 4 domes the oysters were in during the exposure period. Overall, significant differences in biochemical composition (i.e., amino acid content, glycogen, protein, etc.) between the 2 nonparasitized domes or between the 2 snail parasitized domes did not occur more frequently than expected by chance (Binomial Test, $\alpha = 0.05$). Therefore, the two equivalently treated domes of each treatment group (Fig. 1) were lumped together for comparison with precontrol and recovery oysters. Nevertheless, the experimental design represents a case of pseudoreplication; hence the caveats of Hurlbert (1984) should be considered when reviewing the statistical analysis.

RESULTS

Growth, *Perkinsus marinus* Intensity, and Reproduction

Boonea impressa affected oyster growth rate, the intensity of infection by *P. marinus*, and reproductive state. The mean initial shell weights of the precontrol, control, and parasitized groups were not significantly different from each other. By the end of the 4-wk exposure period, both parasitized and unparasitized oysters had gained weight, but oysters parasitized by *B. impressa* gained significantly less weight than unparasitized oysters (Table 1). Oysters with more snails typically gained less weight than oysters with fewer snails. The relationship between the intensity of *B. impressa* parasitism (snail scale) and weight gain among parasitized oysters was significant (Spearman's rank, $P = 0.03$; weight gain normalized to initial weight, $P = 0.001$, Fig. 2).

Mantle cavity volume did not vary among any of the treatment or recovery groups. Condition index was not significantly different between treatment groups or between recovery groups. Condition index was significantly higher in the two recovery

TABLE 1.—Mean and standard deviations for initial shell weight (g) and average shell weight gain per oyster during the 4-wk exposure period and 4-wk recovery period. Significance levels (sig.) from Duncan's multiple range test ($\alpha = 0.05$). A test was restricted to a single column. Groups having the same letter within a column are not significantly different.

	Initial weight		Weight gained during 4-wk exposure		Weight gained during 4-wk recovery	
Group	Mean ± SD	Sig.	Mean ± SD	Sig.	Mean ± SD	Sig.
Precontrol (n = 15)	22.82 ± 12.16	A				
Treatment						
Control (n = 40)	17.16 ± 8.48	A	3.49 ± 1.21	A		
Parasitized (n = 40)	16.84 ± 7.47	A	2.54 ± 1.31	B		
Recovery						
Control (n = 6)					2.16 ± 0.73	B
Previously parasitized (n = 15)					2.89 ± 1.05	A

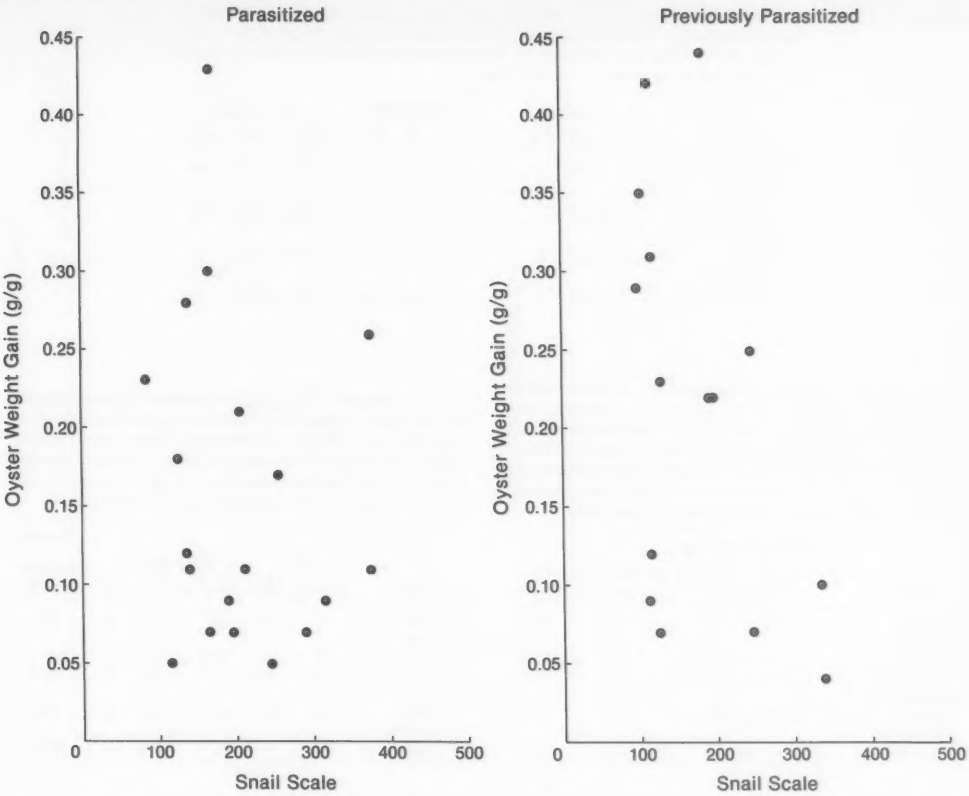

FIGURE 2.—Left: Weight gain (g) per g initial weight of individual snail-parasitized oysters after the 4-wk experimental period as a function of the level of *Boonea impressa* parasitism, or snail scale. Right: Weight gain (g) per g initial weight of individual oysters after the 4-wk recovery period as a function of the level of *B. impressa* (snail scale) during the 4-wk treatment period.

groups than in the treatment and precontrol groups (Table 2).

During the recovery period, when all oysters were parasite-free, the previously parasitized oysters (those with snails during the treatment period) gained significantly more weight than the recovery controls (Table 1). Oysters which were previously parasitized by fewer *B. impressa* during the treatment period gained more weight during the recovery period than those that were previously parasitized by more snails (Spearman's Rank correlation, $P = 0.07$, Fig. 2), but the relationship was considerably weaker than during the treatment period.

The intensity of infection by *P. marinus* increased throughout the experiment in parasitized oysters so that, after recovery, previously parasitized oysters had higher prevalences and intensities of infection than they did after 4 weeks of parasitism; these values in turn were higher than the precontrol values at the experiment's inception (Table 3). Exactly the opposite trend occurred in control oysters. Recovery controls had the lowest values of prevalence and intensity. Consequently, after the recovery period, previously parasitized oysters had significantly higher intensities of infection than recovery controls. The proportion of infected individuals (33% of the controls, 93% of the previously parasitized oysters) was significantly higher as well (χ^2, $P < 0.05$). Within the parasitized oysters, the intensity of parasitism (snail scale) did not correlate with the increase in intensity of *P. marinus* infection during either the treatment or recovery period (Fig. 3, Spearman's Rank, $P > 0.05$; the interaction

TABLE 2.—Means and standard deviations for volume (mL), condition index ($g \cdot mL^{-1}$) and dry weight (g). Significance levels (sig.) from Duncan's multiple range test ($\alpha = 0.05$). A test was restricted to a single column. Groups having the same letter within a column are not significantly different. *n*, see Table 1.

Group	Volume Mean ± SD	Sig.	Condition index Mean ± SD	Sig.	Dry weight Mean ± SD	Sig.
Precontrol	10.4 ± 4.1	A	3.4 ± 0.8	C	0.35 ± 0.14	AB
Treatment						
Control	11.2 ± 3.6	A	5.4 ± 1.0	B	0.34 ± 0.11	AB
Parasitized	9.2 ± 1.7	A	5.5 ± 1.0	B	0.28 ± 0.12	B
Recovery						
Control	9.5 ± 4.6	A	7.1 ± 1.5	A	0.32 ± 0.14	B
Previously parasitized	10.8 ± 3.8	A	7.7 ± 1.5	A	0.51 ± 0.24	A

TABLE 3.—Mean and standard deviations for *Perkinsus marinus* infection intensity among groups. Significance levels from Duncan's multiple range test ($\alpha = 0.05$) apply to the infection intensity data. Groups with the same letter are not significantly different. Percent incidence is the number of oysters infected divided by the number of oysters in the sample. Infection intensity was calculated using the 5-point scale of Mackin (1962). *n*, see Table 1.

Group	*Perkinsus marinus* Infection Intensity Mean ± SD	Significance	Prevalence
Precontrol	1.47 ± 1.45	AB	66.6
Treatment			
Control	1.10 ± 1.06	AB	65.0
Parasitized	1.63 ± 1.32	AB	79.0
Recovery			
Control	0.83 ± 1.60	B	33.3
Previously parasitized	2.21 ± 1.38	A	92.9

TABLE 4.—Results of histological examination of gonadal samples for each group. Significance levels (sig.) from Duncan's multiple range test ($\alpha = 0.05$) are for differences in the number of eggs present per female in a histological section. Percent of females spawning is the number of females with eggs observed in the gonoducts divided by the number of females in the sample.

Group	Sex Female	Male	Eggs present Mean ± SD	Sig.	Percent of females spawning
Precontrol	7	7	31.1 ± 4.4	A	86.0
Treatment					
Control	6	4	36.6 ± 11.0	A	100.0
Parasitized	4	6	21.6 ± 3.9	B	100.0
Recovery					
Control	5	1	37.6 ± 6.0	A	80.0
Previously parasitized	11	4	42.9 ± 9.8	A	81.0

term in the MANCOVA was also nonsignificant).

The number of eggs per microscopic field estimated from histological sections, was significantly lower in parasitized oysters after the 4-wk treatment period (Table 4). No differences between controls and previously parasitized oysters were present after the 4-wk recovery period. The proportion of oysters ready to spawn (female oysters which had eggs visible in the gonoducts) was not significantly different in parasitized and unparasitized oysters during treatment or recovery (χ^2, $\alpha = 0.05$).

Biochemical Composition

Mean levels of the various biochemical components measured in adductor muscle and mantle tissue are given in Tables 5 and 6. A comparison of precontrol, treatment control, and recovery control oysters documents the changes in biochemical composition produced by handling stress and natural environmental changes that occurred during the experiment. Glycogen increased significantly in the mantle tissue during the 4-wk treatment period, then decreased during the recovery period (Table 7). Glycogen in the adductor muscle also decreased during the recovery period (Table 7). Hypotaurine increased in both tissues during the treatment period (Table 8). Most other FAA and the total pool dropped in concentration in the mantle tissue in the first 4 weeks, but then stabilized. In contrast, in the adductor muscle, significant increases in glycine and hypotaurine during the treatment period were offset by a significant decrease in alanine, so the total pool changed little. Again, the FAA pool stabilized during the first 4 weeks. Hence, there was little difference in treatment and recovery controls in any measured biochemical component.

Snail parasitized and control oysters did not differ significantly in the concentration of any of the biochemical components in either the mantle or adductor muscle (Tables 7, 8). Only one biochemical parameter differed between the recovery control

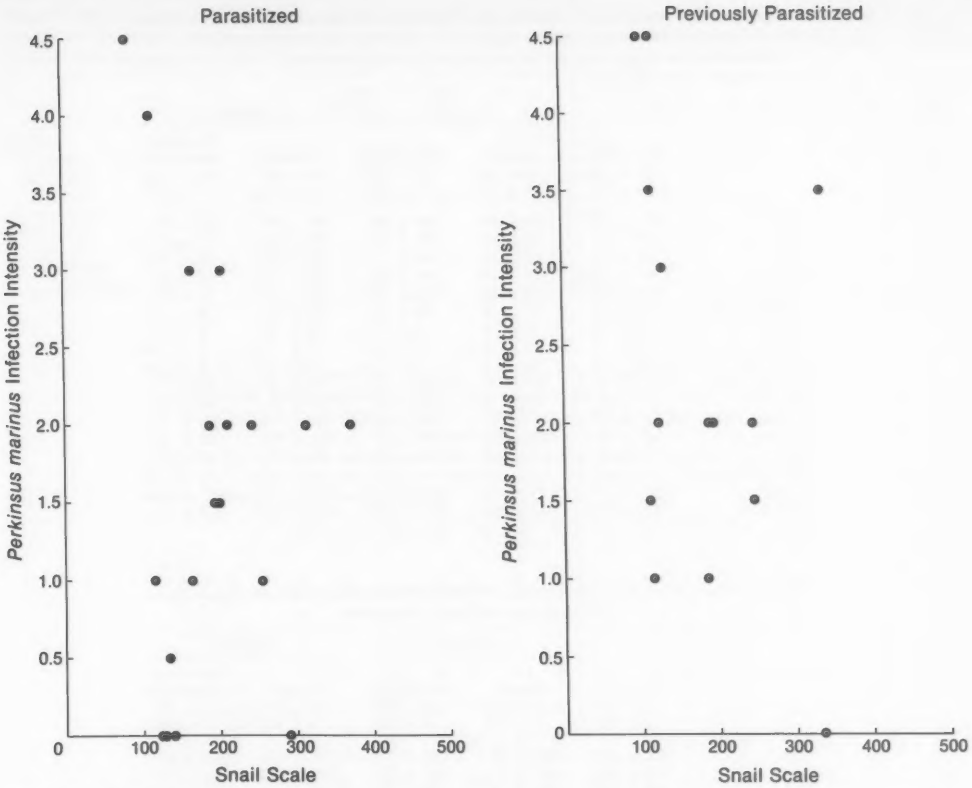

FIGURE 3.—Left: Intensity of *Perkinsus marinus* infection in snail-parasitized oysters as a function of the level of snail parasitism after the 4-wk treatment period. Right: Intensity of *P. marinus* infection in previously snail-parasitized oysters as a function of the level of snail parasitism after the 4-wk recovery period.

and previously parasitized oysters. Recovery controls had significantly less glycogen in the mantle tissue (Table 7). No biochemical component was significantly correlated with the intensity of snail parasitism (snail scale) in parasitized oysters during the 4-wk treatment period except taurine in the adductor muscle (Table 9). A similar comparison, using the previously parasitized oysters after the 4-wk recovery yielded only two significant correlations with snail scale; soluble protein and hypotaurine content. In addition, lipid phosphate in the mantle tissue and fatty acid content in the adductor muscle were significantly correlated with the intensity of *Perkinsus marinus* infection after the recovery period (all recovery oysters, controls and previously parasitized, were included in the analysis, Table 9).

DISCUSSION

Oysters averaged as few as about 3 and as many as 14 snails per day during the 4-wk treatment period; however, only 11% of the oysters had 10 or more snails per day and 76% had fewer than 9 per day. This range of parasitism is typical for many reefs in the experimental area (Copano Bay-Aransas Bay, TX—White et al. 1984; Powell et al. 1987) and corresponds to the lower parasite levels used by White et al. (1988, in press) in laboratory studies on these animals.

The effects of snail parasitism were minor on a biochemical level, but substantial on an organismal level. Growth, reproductive capacity, and health, as measured by *Perkinsus marinus* infection, were significantly affected. Other odostomians also re-

TABLE 5.—Means and standard deviations for all biochemical components in mantle tissue. FAA = total of the 9 free amino acids measured; FAA- = FAA less taurine and hypotaurine; FAA-- = FAA less taurine, hypotaurine, glycine, and alanine; amino acids in μmoles · mL^{-1}; other tissue components in mg · g dry wt^{-1}.

		Treatment		Recovery	
	Precontrol (n = 15) $\bar{x}$ ± SD	Control (n = 10) $\bar{x}$ ± SD	Parasitized (n = 10) $\bar{x}$ ± SD	Control (n = 6) $\bar{x}$ ± SD	Previously parasitized (n = 15) $\bar{x}$ ± SD
FAA	351 ± 94	240 ± 39	280 ± 38	294 ± 64	270 ± 64
FAA-	220 ± 67	116 ± 14	121 ± 15	134 ± 50	117 ± 43
FAA--	57 ± 18	42 ± 6	46 ± 7	49 ± 26	42 ± 13
Taurine	102 ± 33	95 ± 27	119 ± 24	108 ± 15	99 ± 21
Hypotaurine	27 ± 10	39 ± 10	50 ± 23	49 ± 10	54 ± 20
Aspartic acid	22 ± 5	15 ± 2	19 ± 3	22 ± 13	18 ± 5
Serine	8 ± 5	5 ± 2	6 ± 2	5 ± 3	5 ± 3
Threonine	3 ± 1	1 ± 0.2	1 ± 0.7	1 ± 0.4	1 ± 0.5
Glutamine	8 ± 5	2 ± 1	3 ± 0.8	4 ± 3	5 ± 3
Glutamic acid	14 ± 5	16 ± 3	18 ± 5	14 ± 5	12 ± 4
Glycine	71 ± 23	33 ± 5	38 ± 10	44 ± 31	38 ± 17
Alanine	87 ± 33	36 ± 8	38 ± 10	31 ± 10	34 ± 16
Protein	62 ± 45	28 ± 39	60 ± 57	45 ± 40	23 ± 16
Glycogen	28 ± 22	111 ± 59	66 ± 28	37 ± 13	88 ± 48
Lipid phosphate (as PO_4^{-3})	0.62 ± 0.41	0.48 ± 0.27	0.82 ± 0.39	0.5 ± 0.2	0.87 ± 0.54
Fatty acids	20.7 ± 33.1	33.2 ± 49.1	48.7 ± 58.1	9.4 ± 10.5	6.3 ± 3.2

TABLE 6.—Means and standard deviations for biochemical components of adductor muscle tissue. See Table 5 for additional information.

		Treatment		Recovery	
	Precontrol (n = 11) $\bar{x}$ ± SD	Control (n = 10) $\bar{x}$ ± SD	Parasitized (n = 10) $\bar{x}$ ± SD	Control (n = 6) $\bar{x}$ ± SD	Previously parasitized (n = 15) $\bar{x}$ ± SD
FAA	328 ± 119	306 ± 56	289 ± 47	277 ± 110	347 ± 81
FAA-	272 ± 121	227 ± 54	207 ± 35	210 ± 95	266 ± 78
FAA--	57 ± 16	57 ± 8	44 ± 5	75 ± 25	84 ± 24
Taurine	52 ± 17	53 ± 25	66 ± 25	42 ± 16	47 ± 13
Hypotaurine	8 ± 4	22 ± 7	23 ± 3	24 ± 10	33 ± 6
Aspartic acid	17 ± 7	18 ± 4	14 ± 4	18 ± 6	21 ± 8
Serine	5 ± 4	7 ± 3	5 ± 2	27 ± 21	28 ± 21
Threonine	3 ± 1	2 ± 0.9	1 ± 0.5	2 ± 1	3 ± 1
Glutamine	6 ± 2	4 ± 2	2 ± 1	6 ± 4	10 ± 8
Glutamic acid	20 ± 6	18 ± 4	21 ± 6	21 ± 4	20 ± 5
Glycine	54 ± 15	124 ± 37	119 ± 42	85 ± 54	121 ± 44
Alanine	142 ± 63	49 ± 19	39 ± 10	49 ± 30	60 ± 26
Protein	41 ± 13	49 ± 40	45 ± 56	45 ± 35	36 ± 22
Glycogen	6 ± 3	7 ± 3	6.8 ± 0.3	4 ± 2	4 ± 2
Lipid phosphate (as PO_4^{-3})	0.1 ± 0	0.2 ± 0	0.34 ± 0.3	0.25 ± 0.28	0.2 ± 0.1
Fatty acids	15.0 ± 10.0	17.5 ± 16.7	15.3 ± 24.1	6.9 ± 11.5	8.6 ± 16.9

duce host growth rate (Nishino et al. 1983). Oysters parasitized by *Boonea impressa* gained significantly less weight than nonparasitized oysters. Parasitized female oysters had significantly fewer eggs than controls (the effect on males was not quantified).

Reduced growth and impaired reproduction in the host are commonly associated with marine parasites (e.g., Menzel and Hopkins 1955; Cheng et al. 1983; Hawkes et al. 1986). Starvation produces a similar phenomenon (Fair and Sick 1982; Pipe 1985; Wright and Hetzel 1985; Devi et al. 1985). Several lines of evidence suggest that a reduction in net productivity, but not a negative energy balance, produced the results observed here. White et al. (1988) developed an energy flow model for oysters and snails. Using that model, oysters of 4 to 7 cm long, the size we used, would not incur a negative energy balance un-

TABLE 7.—Results of Duncan's multiple range test for biochemical components of the mantle and adductor muscle. Each test considered data for one biochemical component (one vertical group of 5 means) for each tissue. Different letters within a vertical group indicate significant differences at $\alpha = 0.05$ within that group.

	Protein	Glycogen	Lipid phosphate	Fatty acids		Protein	Glycogen	Lipid phosphate	Fatty acids
Mantle					Adductor muscle				
Precontrol	A	B	A	A	Precontrol	A	AB	A	A
Treatment					Treatment				
Control	B	A	A	A	Control	A	A	A	A
parasitized	AB	A	A	A	Parasitized	A	AB	A	A
Recovery					Recovery				
Control	AB	B	A	A	Control	A	B	A	A
Previously parasitized	B	A	A	A	Previously parasitized	A	B	A	A

TABLE 8.—Results of Duncan's multiple range test for free amino acids in the mantle tissue and adductor muscle. Each test considered data for one biochemical component (one vertical group of 5 means) for each tissue. Different letters within a vertical group indicate significant differences at $\alpha = 0.05$ within that group. Tau = taurine; Hyp = hypotaurine; Asp = aspartic acid; Ser = serine; Glu = glutamic acid; Gln = glutamine; Gly = glycine; Ala = alanine; FAA = total for the amino acids measured; FAA- = FAA less taurine and hypotaurine; FAA-- = FAA less taurine, hypotaurine, glycine, and alanine.

	Tau	Hyp	Asp	Ser	Thr	Gln	Glu	Gly	Ala	FAA	FAA-	FAA--
Mantle												
Precontrol	A	B	A	A	A	A	AB	A	A	A	A	A
Treatment												
Control	A	A	B	A	B	B	AB	B	B	B	B	A
Parasitized	A	A	AB	A	AB	B	A	B	B	AB	B	A
Recovery												
Control	A	A	AB	A	B	AB	B	B	B	AB	B	A
Previously parasitized	A	A	AB	A	B	AB	B	B	B	B	B	A
Adductor muscle												
Precontrol	A	C	AB	B	A	A	A	C	A	A	A	BC
Treatment												
Control	A	B	AB	B	AB	A	A	AB	B	A	A	CD
Parasitized	A	B	B	B	B	A	A	AB	B	A	A	D
Recovery												
Control	A	AB	AB	A	AB	A	A	BC	B	A	A	AB
Previously parasitized	A	A	A	A	A	A	A	AB	B	A	A	A

TABLE 9.—Significant *P*-values obtained by MANCOVA from comparison of snail scale and *Perkinsus marinus* infection intensity. Tests using snail scale considered only the parasitized oysters after the treatment period and the previously parasitized oysters after the recovery period. Tests using *P. marinus* considered all oysters, controls and snail parasitized. Abbreviations same as Table 8. M = mantle tissue; A = adductor muscle; — = not significant in either tissue at $\alpha = 0.05$.

	Glycogen	Lipid phosphate (as PO_4^{-3})	Fatty acids	Tau	Hyp	Asp	Thr	Ser	Glu	Gly	Ala	FAA	FAA-	FAA--	Protein
Treatment															
Snail scale	—	—	—	0.02(A)	—	—	—	—	—	—	—	—	—	—	—
Perkinsus marinus	—	—	—	—	—	—	—	0.004(A)	—	—	—	—	—	—	—
Recovery															
Snail scale	—	—	—	—	0.04(A)	—	—	—	—	—	—	—	—	—	0.004(M)
Perkinsus marinus	—	0.03(M)	0.002(A)	—	—	—	—	—	—	—	—	—	—	—	—

til fed upon by at least 25 average-sized (1.75 mm maximum width) snails. Seven snails, a typical value in our experiments, would reduce net productivity by only 5 to 30%, on a daily basis. In addition, condition index and mantle glycogen levels increased during the treatment period in both control and parasitized oysters and the effect of snail parasitism on all biochemical components was small (oysters can regulate some biochemical components even during starvation, Swift and Ahmed 1983; but see Riley 1976).

Consequently, both reduced growth and impaired reproductive capacity can be attributed to a reduction in assimilated carbon available to the host, as a result of either a reduction in filtration rate resulting in less energy being assimilated (Ward and Langdon 1986) or the direct removal of assimilated carbon by the snail. Neither effect was permanent. Growth rate resumed and reproductive state returned to control levels during recovery. In both cases compensatory adjustments occurred during the recovery period so that previously parasitized oysters gained weight and increased egg number faster than the controls. Loosanoff and Nomejko (1955) and Eagle and Chapman (1953) also noted compensatory shell growth in oysters.

Perkinsus marinus infection is an important cause of mortality in oysters (Mackin and Sparks 1962; Mackin 1962; Hofstetter 1977). *Boonea impressa* can transmit *P. marinus* from one oyster to another and can also increase the intensity of infection (White et al. 1987). Continued deterioration after a stress is removed occurs frequently in "recovery" experiments (Kendall et al. 1984; Powell et al. 1984) demonstrating the necessity of examining recovery capacity in acute (vs. chronic) stresses. Growth rate typically recovers more rapidly than most biochemical parameters. In snail-parasitized oysters, both prevalence and intensity of *P. marinus* infection increased during the recovery period. Hence, in contrast to growth rate, no recovery from *P. marinus* actually occurred. By the end of the 8-wk period, infection intensity had increased by about 1 unit on Mackin's (1962) 5 point scale. Growth still occurred and reproductive capacity returned to control levels, however, during this period. These results contradict those of Menzel and Hopkins (1955) who showed that *P. marinus* retarded growth in proportion to the intensity of infection and Mackin (1953) who observed decreased fecundity in heavily infected oysters. Haven (1962) obtained results analogous to ours. Possibly, the oysters in our study were not infected heavily enough to retard growth and reproduction. Mean infection intensity in previously parasitized oysters after the recovery period was only 2.2, a light to moderate infection.

Changes observed at the biochemical level among the previously parasitized oysters after the recovery period, particularly in fatty acid and lipid phosphate content, were related to increased infection intensity of *P. marinus* (Table 9). Stein and Mackin (1955), Mackin (1962), and White et al. (in press) also noted changing lipid levels related to infection intensity. Lipid phosphate is predominantly a structural component whereas fatty acids, usually as triglycerides, are storage materials in many marine invertebrates (Gabbott 1976; Trider and Castell 1980; Gehron and White 1982). The increased lipid phosphate content in mantle tissue, however, probably indicates an increase in structural material, noted histologically by Stein and Mackin (1955, 1957) to occur in conjunction with *P. marinus* infections.

Glycogen is the primary storage material in most bivalves (Beninger and Lucas 1984). Parasitism frequently affects carbohydrate metabolism (Cheng 1963; Mohamed and Ishak 1981; Thompson and Binder 1984; Thompson 1986). White et al. (in press) suggested that *P. marinus* alters oyster metabolism favoring gluconeogenesis. Our results support this hypothesis. Glycogen levels dropped only in recovery control oysters in which *P. marinus* infection intensity also declined. Changing fatty acid content might be similarly explained. In contrast, Stein and Mackin (1957) noted decreased glycogen levels in heavily infected oysters (3 to 5 on Mackin's scale). Few of our oysters were this heavily infected, however. An alternative explanation, that slower reproductive development in parasitized oysters was responsible for variation in glycogen and fatty acid content, cannot be completely excluded because *P. marinus* infection intensity did not correlate with glycogen levels in recovery oysters. Parasitized oysters had fewer eggs than control oysters, however. Additionally, neither the number of eggs present nor the number of oysters spawning differed significantly between control and previously parasitized oysters during the recovery period.

Results of previous workers suggest that significant decreases in storage compounds, whether caused by *B. impressa* or *P. marinus*, only occur in heavily infected animals (e.g., Stein and Mackin 1957; White et al. in press). This, too, is true for the amino acid pool where significantly decreased levels are usually associated with more severely stressed animals (e.g., Powell et al. 1982, 1984). The few significant effects on amino acids in this study, like all the other biochemical components measured,

were produced by increases in concentration. Soniat and Koenig (1982) observed significant changes in the free amino acid pool due to *P. marinus*, particularly in taurine concentration. We noted changes in taurine during the treatment period and hypotaurine during recovery in the adductor muscle but these were related to snail parasitism.

Biochemical components, though rarely significantly affected, were affected not just in the mantle tissue but also in the adductor muscle. One possibility, that the snail's effect is localized at the point of feeding, is not supported by the data. Snail parasitism produces systemic effects.

CONCLUSIONS

Complementary results of White et al. (1984, 1988, in press) and this study permit a general description of the impact of snail parasitism on oysters at normal field levels. Both growth rate and reproductive development slow significantly, but recover rapidly once the snails are removed. Hence, the temporal stability of snail patches must determine the cumulative effect on field populations of oysters. The prevalence and intensity of infection by *Perkinsus marinus* is significantly increased, but recovery does not occur. That is, *Boonea impressa* probably facilitates and encourages the normal spread and intensification of *P. marinus* from which oysters, if they recover, only do so the following winter when low temperatures typically reduce infection levels (Hewatt and Andrews 1956; Burrell et al. 1984; Soniat 1985). This effect, then, is long term. Most changes in biochemical components were due to infection by *P. marinus*. Snail feeding reduces net productivity but, at normal field levels, starvation is an unlikely result. Increased infection by *P. marinus* typically raises glycogen and lipid levels, at least in light to moderate infections. Of the free amino acids, taurine and hypotaurine have been shown to be affected by *P. marinus* and *B. impressa*. Little change in the remaining FAA or the total pool has been observed singly or in concert. Feng et al. (1970) noted increased taurine levels in oysters parasitized by *Bucephalus* sp. and *Minchinia nelsoni*. Hence, an increase in taurine and hypotaurine levels apparently is a general response to parasitism in oysters.

Yuill (1987) emphasized the importance of subtle effects produced by parasites on host populations. *Perkinsus marinus* is an important source of mortality in oyster populations (Mackin and Sparks 1962; Mackin 1962; Hofstetter 1977). Data suggest that one of the most important aspects of parasitism by *B. impressa* is to encourage this second parasitic organism. To this extent, over the year, *B. impressa* at normal field densities could be responsible for a substantial amount of mortality in oyster populations.

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LIFE TABLES FOR TWO FIELD POPULATIONS OF SOFT-SHELL CLAM, *MYA ARENARIA*, (MOLLUSCA : PELECYPODA) FROM LONG ISLAND SOUND

DIANE J. BROUSSEAU[1] AND JENNY A. BAGLIVO[2]

ABSTRACT

Life tables were constructed for two populations of *Mya arenaria* from Long Island Sound, USA, based on schedules of age-specific fecundity and mortality determined under natural conditions. *Mya arenaria* shows a basic conservatism in general life history pattern. In both populations, fecundity increases with increasing female size; sexual maturity is attained at 1 year of age; a single annual breeding season occurs and survivorship curves approximate the type III of Deevey, which is characterized by extremely heavy mortality early in life followed by relatively constant mortality thereafter. Differences in the age-specific parameters for the two populations exist, however; for clams greater than 1 year of age, both age-specific fecundity and survivorship are significantly higher in the Stonington population. These differences in the structure and dynamics of the two populations may be due to environmental heterogeneity. Reduced body size due to slower growth in coarse substrate, as well as the increased maintenance demands resulting from burrowing and valve activity in large-grained sediment, may account for the lower egg production and lower survival rates found in the Westport population.

The life history pattern of a species has been defined as the way in which that species partitions the limited resources of time or energy among the three basic biological processes of growth, maintenance, and reproduction. Efforts to generate empirical values for life history parameters, age-specific fecundity and survivorship, have only recently allowed the construction of life tables for field populations. Determining life history parameters for a commercially important species such as the soft-shell clam, *Mya arenaria*, is particularly useful since they can be used in theoretical models which are designed to analyze the effect of changing survival and fecundity values on the growth rate of the population.

Life tables now exist for a number of benthic marine invertebrates: the barnacle—*Chathamulus stellatus* (Connell 1961); the prosobranchs—*Dicathais orbita* (Phillips and Campbell 1974), *Nucella* (= *Thais*) *lapillus* (Frank 1969), *Nodilittorina tuberculata* (Doran 1968), and *Conus pennaceus* (Perron 1983); the coelenterates—*Muricea californica* (Grigg 1977), *M. fruticosa* (Grigg 1977), and *Balanophyllia elegans* (Fadlallah 1983); the bivalves—*Mya arenaria* (Brousseau 1978), *Tapes phillipinarum* (Yap 1977), and *Gemma gemma* (Weinberg 1985). These studies, however, examine life history parameters for a single species population or for successive cohorts within a population.

The present study examines age-specific fecundity and survivorship in two geographically separated populations of the soft-shell clam, *Mya arenaria*, using identical methodology. Since differences in methodology can influence estimates of demographic parameters (Fadlallah 1983) uniformity of approach is necessary for interpopulation comparisons. This study is the first reported examination of species-specific traits in two naturally occurring populations and was carried out as part of a broader study of the population dynamics of this species along the Connecticut shore of Long Island Sound.

MATERIALS AND METHODS

Field Study Areas

Field studies were conducted at two intertidal sites in Long Island Sound, one located at Barn Island in Stonington, CT (lat. 41°20′N; long. 71°53′W) and the other in the Saugatuck River in Westport, CT (lat. 41°06′N; long. 73°23′W) (Fig. 1). The Stonington site is a narrow intertidal sandflat which extends approximately 10 m shoreward to a coarse sand beach. At low tide the Westport site extends 30 m (at its widest point) shoreward to a *Spar-*

[1]Department of Biology, Fairfield University, Fairfield, CT 06430.
[2]Department of Mathematics and Computer Science, Fairfield, University, Fairfield, CT 06430; present address: Mathematics Department, Boston College, Chestnut Hill, MA 02167.

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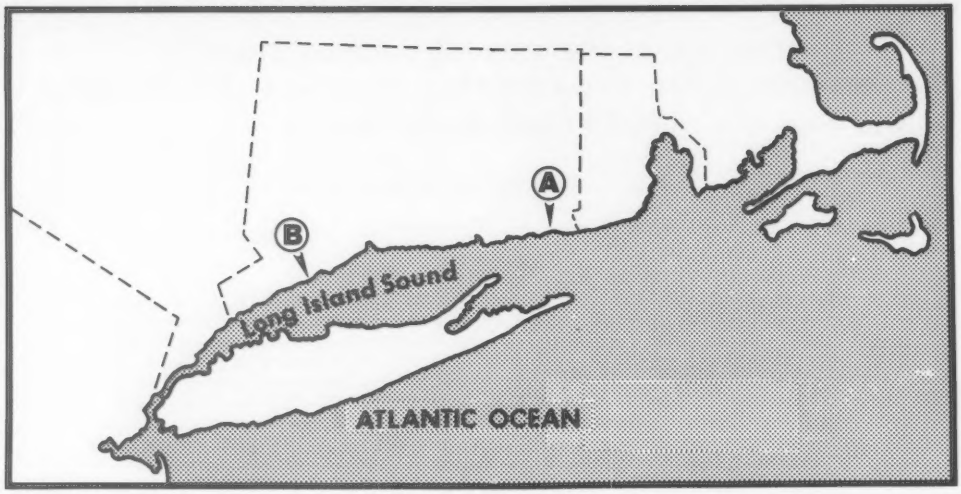


FIGURE 1.—Map showing locations of the two study sites: Barn Island in Stonington, CT (A) and Saugatuck River in Westport, CT (B).

tina alterniflora marsh. The substrate there is coarser than at the Stonington site; 50% by weight is >4 mm grain size diameter, much of that classifiable as either cobble or boulder (Brousseau and Baglivo 1987). Both study sites are closed to shellfish harvesting to high levels of bacterial contamination.

Although annual salinity and temperature profiles for the two sites are not available, monthly surface and bottom salinity and temperature readings for the period March 1979–June 1981 and October 1985–August 1986 are available for four sites in western Long Island Sound: Norwalk, CT (lat. 41°02.5′N; long. 73°27.2′W), Bridgeport, CT (lat. 41°08.7′N; long 73°11.1′W), Stratford, CT (lat. 41°07.6′N; long. 73°07.6′W), and New Haven, CT (lat. 41°14.4′N; 72°54.2′W) (Tettlebach et al., 1984; Blogoslawski, pers. comm.[3]). All water sampling was done at spring low tide in approximately 20 ft of water. The annual average range of surface temperatures for the four sites was 0.5°–24.2°C. The lowest surface temperature, 0.0°C, was recorded at the New Haven station in February 1980; the highest was 25.0°C recorded at the Stratford station in August 1986. Annual average range of bottom temperatures was 0.6°–23.4°C. Surface salinities ranged from 16.9 to 33.3‰ with a low of 15.9‰ reported for Stratford and a high of 35.7‰ recorded at the Norwalk station. Mean bottom salinities during that period ranged between 17.0 and 34.4‰.

[3]W. Blogoslawski, Northwest Fisheries Center Milford Laboratory, National Marine Fisheries Service, NOAA, Roger Avenue, Milford, CT 06460, pers. commun. March 1987.

Fecundity

Oocyte production by female clams collected during the summer spawning seasons of 1984 and 1985 was estimated using a histological technique (Brousseau 1976). One hundred twenty-five gravid females from the Westport population and 123 from the Stonington population were examined. Size-specific fecundity rates were converted to age-specific rates using age-size information for *M. arenaria* obtained from analysis of internal shell growth bands (Brousseau and Baglivo 1987). Age-specific fecundity estimates for x-yr-old clams, m_x, were calculated using the formula:

$$m_x = 0.5 \sum m_i \, P(\text{size-class } i \mid x \text{ yr-old}) \quad (1)$$

where m_i is the mean fecundity for size-class i, P(size-class i | x-yr-old) is the conditional probability that an x-yr-old clam is in size-class i, and the sum is taken over 10 mm size-classes i. The conditional probabilities P(size-class i | x-yr-old) were derived empirically (see Appendix Tables 1, 2). Ten millimeter size-classes were used because of sparseness in the data. By convention, m_x represents the

total number of eggs produced by a female of age x which may be considered to be "female eggs". Because the sex ratio of both populations is 1:1 (Brousseau 1987a), only half of the oocytes produced will eventually become females. Accordingly, each m_x is one-half the total annual fecundity per female of age x.

Mortality

To determine size-specific 1-yr survival rates of adult clams (>1 year of age), *M. arenaria* from Stonington and Westport were collected, individually tagged, and returned to their original sites (Stonington: 31 May–1 June 1985; Westport (Plot A): 1 May 1984 and Westport (Plot B): 22 May 1984). Clams were measured to the nearest 0.1 mm anteroposteriorly and marked for identification using a method described previously (Brousseau 1979). Tagged clams were replanted in parallel furrows excavated to a depth of 20–30 cm. All plots were 0.3 m apart and located at midtide level (+3.0 m). At the end of the test period, the clams were collected. All numbered individuals, both alive and dead, were returned to the laboratory for measurement. A total of 1,049 clams from the Stonington population were tagged, of which 78% were recovered. One-year recovery rate at the Westport site was 40% of the 1,977 clams initially planted. Mortality rates were determined on the basis of the number of clams recovered. This method gives a more accurate estimate of mortality since it does not consider clams that were not recaptured in these estimates.

If, on recapture, a dead clam showed no evidence of growth, either death had occurred naturally in a slow-growing individual or premature death had occurred as a result of trauma due to the marking procedure. In order to correct for premature mortality caused by handling, the proportion of live clams which showed an increase in shell length over the year was calculated (Table 1). For the Westport population all live clams <40 mm shell length grew, while 94.7% of live clams over 40 mm grew. For the Stonington population all live clams <50 mm shell length had grown during the year, while 91.9% of live clams over 50 mm grew. In order to estimate size-specific survivorship then, the following rules were applied:

TABLE 1.—Distribution of *Mya arenaria* recovered alive showing growth and no growth during the test period.

	Westport (clams >40 mm)		Stonington (clams >50 mm)	
	Growth	No growth	Growth	No growth
Number	196	11	440	39
Percent	94.7	5.3	91.9	8.1

Westport:

$$\text{Classes <40 mm: } P(\text{surviving one year}) = N_A/(N_A + N_{DG}) \quad (2)$$

$$\text{Classes >40 mm: } P(\text{surviving one year}) = N_A/(N_A + N_{DG}/0.947)$$

Stonington:

$$\text{Classes <50 mm: } P(\text{surviving one year}) = N_A/(N_A + N_{DG}) \quad (3)$$

$$\text{Classes >50 mm: } P(\text{surviving one year}) = N_A/(N_A + N_{DG}/0.919)$$

where N_A is the number alive and N_{DG} is the number dead with growth. In the smaller classes (Westport, <40 mm; Stonington, <50 mm), the sum $N_A + N_{DG}$ represents all recovered individuals, while in the larger classes, the adjustment factor allows us to add a number of dead without growth back into the total recovered in the same proportion as the live with no growth.

Age-specific survival rates, P_x, were based on the same age-size information used to determine age-specific fecundity rates. These rates were calculated using the formula:

$$P_x = \sum p_i \, P(\text{size-class } i \mid x\text{-yr-old}) \quad (4)$$

where p_i is the probability that a clam in size-class i survives one year, $P(\text{size-class } i \mid x\text{-yr-old})$ is the conditional probability that an x-yr-old clam is in size-class i, and the sum is taken over 10 mm size classes i.

The probability of surviving from settlement to one year (a period of about 10 months) is calculated from the estimates of the density of the population in 2 consecutive years. Both populations were sampled during periods of maximum settlement in 1985. This period occurred approximately 3 weeks earlier in the Westport population. At each sampling, 18 to 35 samples (0.1 m^2 × 30 cm deep) were taken along transects running from mean low water shoreward to the mean high water mark. Samples were wet-seived in the laboratory (2 mm mesh) and the shell lengths of the clams retained by the seive were measured. Clams of size 2–20 mm in the first year of sampling are assumed to be the spat; those of size 20–50 mm the following year are assumed to have come proportionately from the settlement of the previous year in the same ratios as the empirical probability distributions (Appendix Tables 1, 2).

RESULTS

Fecundity

Fecundity of *Mya arenaria* increased with increasing female body size (Fig. 2). Size-specific fecundity schedules, however, differed at the two study sites. Comparison of regression lines for log(fecundity) vs. shell length by analysis of covariance indicated that the relationships were significantly different ($P = 0.004$). Size-specific oocyte production in the Stonington clams was larger than in clams from Westport. The smallest gravid females observed were 34 and 27 mm in shell length in the Stonington and Westport populations, respectively. Age at first reproduction is 1 year in clams from both sites. Sex ratios in both populations did not differ significantly from 1:1 (Brousseau 1987a).

Recruitment and Mortality

Both temporal and spatial variations in annual recruitment were observed during the study period. A substantial settlement occurred at the Westport site in 1985, as evidenced by the high densities of 2–20 mm clams present in late July of that year (Table 2). In contrast, spat densities at the Stonington site were low in early August of 1985, when settlement occurred. Nonetheless, persistence of the 1985 year class at Westport was poor, whereas approximately one-half of those set in the Stonington population during that year were alive one year later. The coarse substrate at the Westport site may have aided attachment of the byssal stage juveniles, resulting in the higher recruitment rate during the summer of 1985. Direct estimates of *M. arenaria* survivorship during the postsettlement to 1-yr

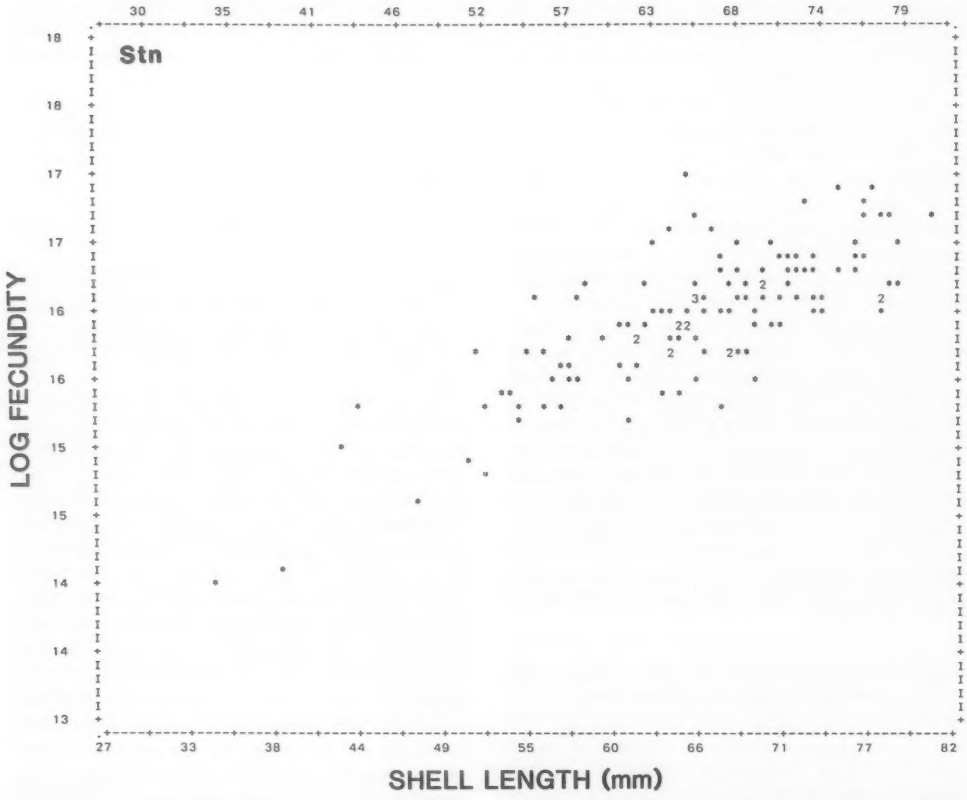


FIGURE 2.—Log of fecundity versus shell length for *Mya arenaria* from

TABLE 2.—Densities per 0.1 m^2 of *Mya arenaria* in size-classes 2–50 mm in the Westport and 2–60 mm in the Stonington populations in 1985 and 1986.

Location and date	Samples	Size-class (mm)	*N*/0.1 m^2	(range)
Westport, Connecticut				
23 July 1985	28	2–20	23.36	(0–84)
09 June 1986	18	10–20	0.11	(0–1)
		20–30	0.44	(0–5)
		30–40	0.89	(0–4)
		40–50	0.50	(0–3)
Stonington, Connecticut				
15 Aug. 1985	35	2–20	0.37	(0–7)
24 June 1986	24	20–30	0.04	(0–1)
		30–40	0.13	(0–1)
		40–50	0.33	(0–2)
		50–60	0.75	(0–3)

period (10 months) obtained by dividing the number of 1-yr-olds alive in the summer 1986 by the estimated cohort size in the previous year were 0.0283 and 0.5869 for the Westport and Stonington populations, respectively.

Size-specific survival rates of adult clams (≥1 year) at both sites are shown in Tables 3 and 4. These represent empirical estimates from mark and recapture studies with survival adjustments in the larger classes made according to Equations (2) and (3). Statistical comparison of the survival distributions of adult clams, however, was limited to those recovered live or recovered showing some growth. At the Westport site survival was constant across the 10 mm size classes: 20–29 through 50–59 and 60+. At Stonington, however, the size-specific survival for classes 30–39 through 70–79 and 80+ increased slightly with size ($P < 0.05$, χ^2 test). The probability

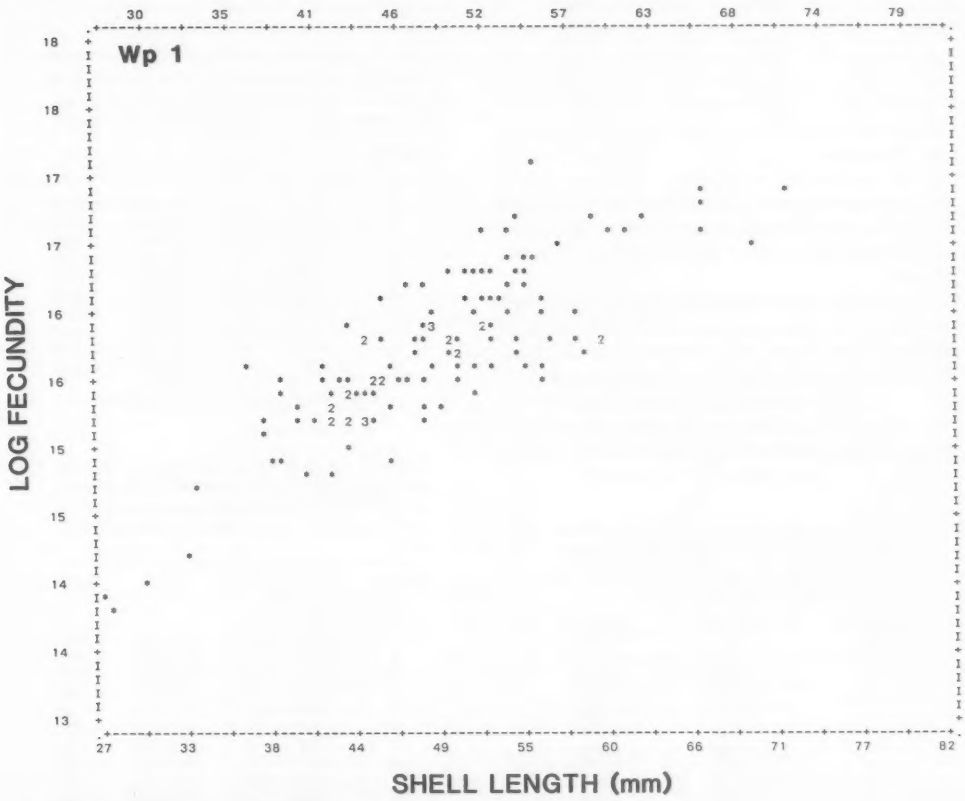


FIGURE 2.—*Continued*—the Stonington (STN) and Westport (WP1) populations.

TABLE 3.—Size-specific survival rates for marked *Mya arenaria* from the Stonington population. P = probability of an individual from size-class i surviving one year; N_A = number of live clams; N_{DG} = number of dead clams showing growth.

Size-class	Size (mm)	N_A	N_{DG}	P
2	20–30			
3	30–40	23	3	0.8846
4	40–50	106	18	0.8548
5	50–60	134	7	0.9462
6	60–70	161	11	0.9308
7	70–80	159	9	0.9420
8	80+	25	0	1.0000

TABLE 4.—Size-specific survival rates for marked *Mya arenaria* from the Westport population. P = probability of an individual from size-class i surviving one year; N_A = number of live clams; N_{DG} = number of dead clams showing growth.

Size-class	Size (mm)	N_A	N_{DG}	P
2	20–30	15	5	0.7500
3	30–40	87	56	0.6084
4	40–50	150	76	0.6515
5	50–60	48	19	0.7052
6	60–70	9	5	0.6303
7	70–80	0	0	0.0000
8	80+			

of surviving one year for adult clams at Stonington (30+ mm in shell length) is significantly higher than at Westport (20+ mm in shell length) ($P < 0.001$, χ^2 test).

Age-specific survivorship estimates (Table 5) were calculated by assuming that 20–30 mm clams at Stonington survivied with the same probability as 30–40 mm clams and that 90–100 mm clams at Stonington survived with the same probability as 80–90 mm clams and application of Equation (4) using the empirical distributions in Appendix Tables 1 and 2.

TABLE 5.—Age-specific survival rates for marked *Mya arenaria* from the Westport and Stonington, CT populations. P_x = probability of surviving from age-class x to age-class $x + 1$.

Age-class (yr)	Westport P_x	Stonington P_x
1	0.6390	0.8843
2	0.6442	0.9307
3	0.6625	0.9390
4	0.6680	0.9550
5	0.6595	0.9661
6	0.6422	0.9746
7	0.6128	0.9746
8	0.5991	0.9746
9	0.5021	0.9746

Population Dynamics

The age-specific survivorship and fecundity schedules for *M. arenaria* are combined in life table form in Tables 6 and 7. Since rates of larval survivorship are difficult to measure for species with planktonic larvae, simplifying assumptions are necessary for estimating survivorship probabilities of larvae (age 0). In order to complete the life tables the equilibrium settlement rates (r_s) were calculated using the method of Brousseau et al. (1982). Our choice of r_s implies that the net reproductive rate, R_0, which is defined by $R_0 = \sum l_x m_x$, were l_x = survivorship and m_x = fecundity, equals one for both populations. This is not meant to imply however, that the populations studied here are considered to be in equilibrium. Rather, it is used simply as a theoretical construct in which to examine possible consequences of differing fecundity and mortality schedules on the two populations of *M. arenaria*.

TABLE 6.—Life table for the Westport, CT *Mya arenaria* population, assuming equilibrium conditions. l_x = survivorship to beginning of age interval x, or $l_{x-1} \times P_{x-1}$ when $x > 1$; m_x = fecundity during age interval x.

Age (yr)	l_x	m_x	$l_x m_x$
0	1.0		
1	[1]1.0599×10^{-7}	1485615	0.1575
2	6.7728×10^{-8}	2989512	0.2025
3	4.3630×10^{-8}	3867846	0.1688
4	2.8905×10^{-8}	5192053	0.1501
5	1.9309×10^{-8}	5892286	0.1138
6	1.2734×10^{-8}	6464925	0.0823
7	8.1780×10^{-9}	6478050	0.0530
8	5.0115×10^{-9}	6842903	0.0343
9	3.0024×10^{-9}	8390977	0.0252
10	1.5075×10^{-9}	8390977	0.0126

[1] $l_1 = r_s \times$ (probability of surviving from 2 months to 1 year).

TABLE 7.—Life table for the Stonington, CT *Mya arenaria* population, assuming equilibrium conditions. l_x = survivorship to beginning of age interval x, or $l_{x-1} \times P_{x-1}$ when $x > 1$; m_x = fecundity during age interval x.

Age (yr)	l_x	m_x	$l_x m_x$
0	1.0		
1	[1]2.014×10^{-8}	1109952	0.0224
2	1.7811×10^{-8}	3712746	0.0661
3	1.6577×10^{-8}	4947569	0.0820
4	1.5566×10^{-8}	7125027	0.1109
5	1.4866×10^{-8}	8287563	0.1232
6	1.4362×10^{-8}	8724158	0.1253
7	1.3997×10^{-8}	8724158	0.1221
8	1.3642×10^{-8}	8724158	0.1190
9	1.3296×10^{-8}	8724158	0.1160
10	1.2958×10^{-8}	8724158	0.1130

[1] $l_1 = r_s \times$ (probability of surviving from 2 months to 1 year).

The equilibrium settlement rate (r_s) for the Westport population is 3.7453×10^{-6} and that for the Stonington population is 3.4318×10^{-8}. The equilibrium first year survival rates (i.e., the probability of surviving from egg to year 1 necessary to maintain a population at equilibrium) then, become 1.0599×10^{-7} and 2.014×10^{-8} for the Westport and Stonington populations, respectively.

Under the assumption of equal rates of larval import and export, it is possible to calculate empirical settlement rates by estimating the total number of eggs released per unit area by spawning females in 1985 and dividing this value into the densities of 2–20 mm spat settled per unit area 2 months later. Size-frequency data for the populations was used to determine the number of clams in each 10 mm size class (Fig. 3). The number of animals in each class (assuming that one-half the population is female) was multiplied by the mean size-specific annual fecundity value for that size class. Summing over all size classes of reproducing females gives an estimate of the 1985 oocyte production per unit area. Empirical settlement rates of 8.4589×10^{-6} and 7.1953×10^{-8} were calculated for the Westport and Stonington populations. These represent values of 2.2585 and 2.0967 times the estimated equilibrium settlement rate of these populations. Multiplying the empirical settlement rate by the probability of surviving the remainder of the year give actual first year actual first year survival rates of 2.3939×10^{-7} and 4.2229×10^{-8} for Westport and Stonington, respectively.

The heavy mortality evident by the low juvenile survivorship rates (l_1) for *M. arenaria* take into account the losses incurred during fertilization, metamorphosis and recruitment, and subsequent survival through the first year of life. Table 8 compares the first year survival rates of representative marine invertebrate species with planktonic and nonplanktonic modes of development. Early survival in species lacking planktonic larvae is on average, three orders of magnitude higher than that of species which pass through a planktonic larval stage.

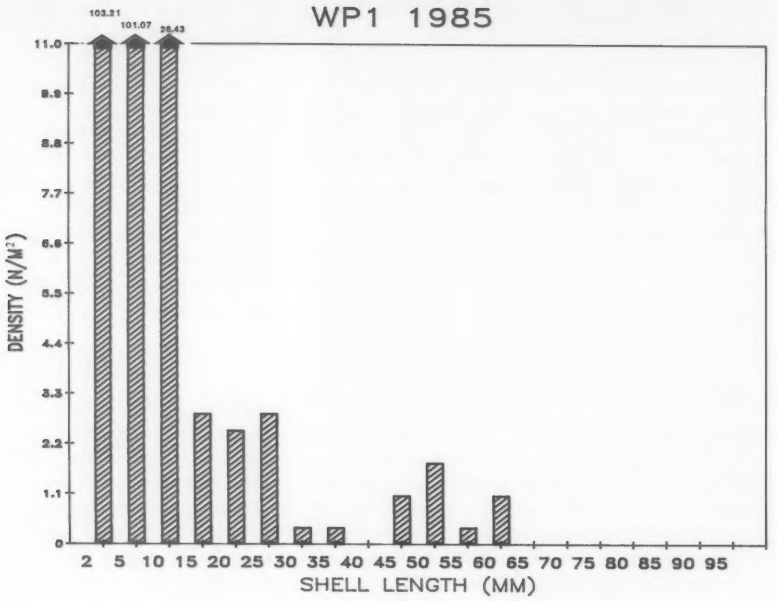
DISCUSSION

General comparisons of life history traits are useful but quantitative comparisons are possible only from the more detailed information found in life tables (age-specific fecundity and survivorship). The difficulty in generating such information, especially for marine bivalves, many of which have planktonic larval stages during their life cycles, has resulted in the construction of few complete life tables. Moreover, no reported field study has examined life history traits for more than one population of a species simultaneously. Consequently, the extent to which quantitative differences in life history parameters are characteristic of the life history of a single species is unknown.

TABLE 8.—Empirical estimates of first year survival rates of marine invertebrate species with and without planktonic larvae (adapted from Perron 1983).

Class	Species	Survivorship l_1	Developmental mode	References
Anthozoa	*Muricea californica*	2.6×10^{-7}	planktonic	Grigg (1977)
	Muricea fruticosa	3.7×10^{-6}	planktonic	Grigg (1977)
	Balanophyllia elegans	5.0×10^{-2}	nonplanktonic	Fadlallah (1983)
Bivalvia	*Gemma gemma*		nonplanktonic	Weinberg (1985)
	Cohorts 1978–1981	2.3×10^{-2}		
		1.2×10^{-1}		
		2.0×10^{-1}		
		1.1×10^{-1}		
	Mya arenaria		planktonic	Present study
	Westport population	$2.4 = 10^{-7}$		
	Stonington population	4.2×10^{-8}		
	Tapes phillipinarum	1.8×10^{-6}	planktonic	Yap (1977)
Gastropoda	*Thais lamellosa*	[1]9.0×10^{-3}	nonplanktonic	Spight (1975)
	Conus pennaceus	7.0×10^{-4}	nonplanktonic	Perron (1983)
	Lacuna pallidula	2.0×10^{-4}	nonplanktonic	Smith (1973)
	Aplysia juliana	[2]8.4×10^{-7}	planktonic	Sarver (1979)
Crustacea	*Balanus glandula*	6.0×10^{-5}	planktonic	Connell (1970)
	Barnacles (3 spp.)	2.0×10^{-5}	planktonic	Hines (1979)

[1]Does not include prehatching mortality.
[2]Survival through 30-d planktonic period only.



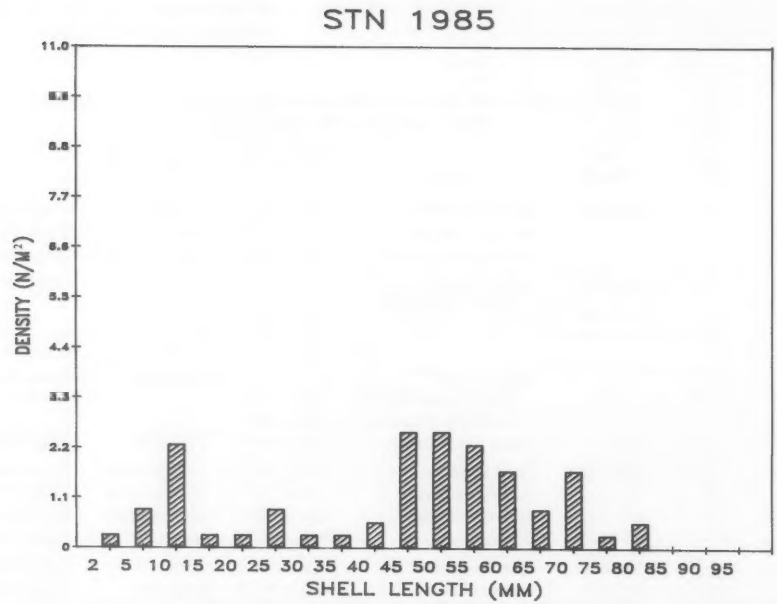
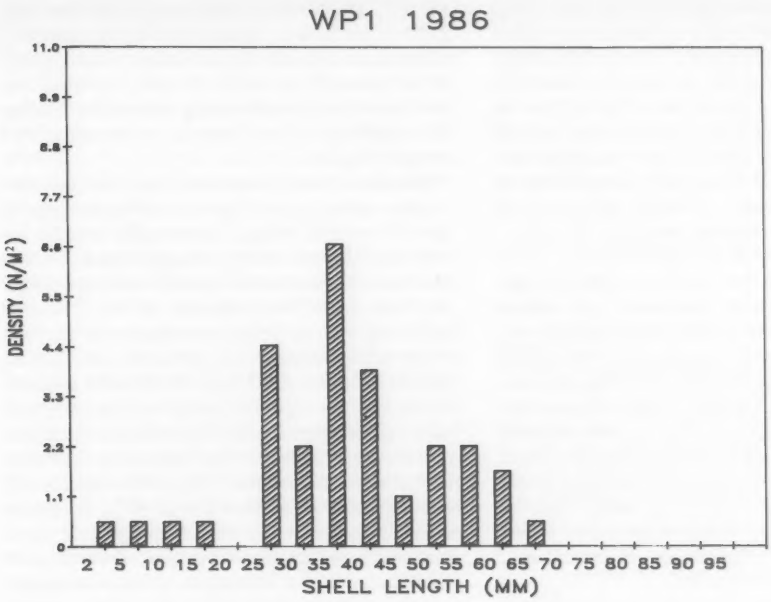


FIGURE 3.—Size-frequency distributions of *Mya arenaria* from the Stonington (STN)



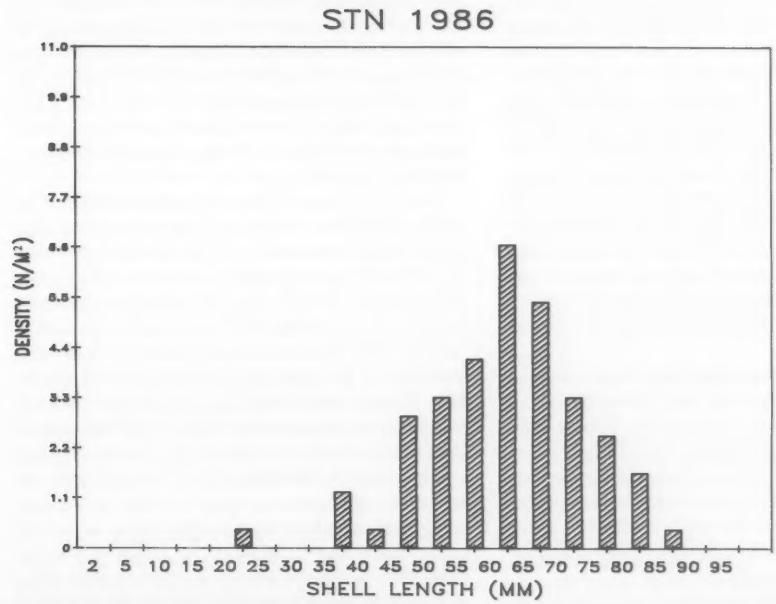


FIGURE 3.—*Continued*—and Westport (WP1) populations in 1985 and 1986.

The two populations of *M. arenaria* from Long Island Sound appear to show a basic conservatism in general life history pattern. In both populations, fecundity increases rapidly in young females with individuals reaching sexual maturity in time to reproduce at the beginning of their second year of life. Similarly, larval and adult survivorship schedules follow the type III survivorship curve of Deevey (1947). Extremely heavy mortality early in life is followed by roughly constant mortality thereafter. This pattern is similar to that described for a population of *M. arenaria* from Gloucester, MA (Brousseau 1978) except that in the latter, age of first reproduction occurs at the end of the second year. It is interesting to note, however, that some of the major life history features of *M. arenaria* show considerable latitudinal variation within the species. Frequencies of spawnings during the year increases (for review see Ropes and Stickney 1965; Brousseau 1987a) and length of life and body size show a tendency to decrease with decreasing latitude (Belding 1930; Newcombe 1935). Details of the ways in which such variations affect the life history parameters, however, remain to be studied.

The possibility of gene flow between populations of animals with planktonic larval stages always exists. Nevertheless, the amount of genetic overlap is effectively reduced as the geographical distance between the populations increases. The significant quantitative differences in the age-specific demographic parameters for the two populations studied here suggest that within the framework of a general life history strategy, a response to the biotic and abiotic components of the immediate environment is possible. Evidence from this study indicates that environmental conditions at the Westport site may be less optimal for the growth and maintenance of *M. arenaria* than are those at the Stonington site. The higher equilibrium settlement rate calculated for the Westport population indicates that on average, a larger annual spatfall is needed to maintain that population than is required at the Stonington site.

The biotic factors most often cited as agents capable of altering the survival and fecundity of individuals are predation, competition, disease, and parasitism. It is unlikely that predation was a major source of adult mortality at either site for reasons previously discussed. Moreover, the effects of predation would be limited to the small, surface-dwelling clams, since 1) crabs, fish, and birds are unable to capture deep burrowing adults and 2) it has been demonstrated that *M. arenaria* exhibits a "size refuge" from naticid predators (Edwards and Hueb-ner 1977). Hancock (1973) has suggested that competition for food or space between the spat and adults may contribute to lowered survival in newly settled clams. If this were the case, one would expect lower juvenile survivorship rates in the Stonington population where population densities were greater (Fig. 3).

Trematode infestations have been demonstrated to cause castration and high mortalities in a population of venerid clams, *Transenella tantilla*, in California (Obrebski 1968). Although both trematode infections (Stunkard 1938; Uzmann 1951) and fungal parasites have been reported in *M. arenaria* (Andrews 1954), no evidence of either was observed in the 2,826 histologically prepared clams (1,583 from Stonington; 1,243 from Westport) examined in a study of the reproductive cycle in the two populations (Brousseau 1987a). Sarcomatous neoplasia, a proliferative disorder characterized by increased number of "leukemia-like" cells in the tissues and organs (Farley 1969; Brown et al. 1977; Cooper et al. 1982), has been identified in samples of clams from both Stonington and Westport. Prevalence of the disorder in the Stonington population ranges from 0 to 46%, whereas 0–69% of the *M. arenaria* from Westport were neoplastic, depending on the collection date (Brousseau 1987b). At present it is not known if neoplasia is a source of mortality in field populations of clams. It seems reasonable to assume that it is, however, since neoplastic cells are invasive and at times cause the destruction of organs and tissues in infected animals (Yevich and Barszcz 1977). If sarcomatous neoplasms prove to be malignant, this disease could be responsible to some degree for the higher mortality rates reported in the Westport population.

The abiotic factors with the greatest effect on the biotic potential of estuarine organisms are temperature, salinity, substrate, and food availability. Adult *M. arenaria* typically inhabit the intertidal zone and are adapted to a wide range of fluctuations in water temperature and salinity. In addition, sediments tend to buffer temperature and salinity fluctuations (Sanders et al. 1965; Johnson 1965, 1967). Therefore, infaunal organisms like the soft-shell clam are subject to less extreme environmental fluctuations than are exposed organisms living on or attached to the surface. Belding (1930) noted that *M. arenaria* withstands extreme variation in salinity, being able to adjust to changing tides every six hours. Shaw and Hamons (1974) found that lethal conditions for burrowed clams were met only when temperatures persisted in the high 20°C range and salinities were 2‰ or lower. In the laboratory,

adult survival is not altered by salinities of 2.5‰ (Chanley 1957; Pfitzenmeyer and Drobeck 1963; Castagna and Chanley 1973) to 35‰ (Castagna and Chanley 1973). Annual water temperature and salinity patterns in Long Island Sound fall well within the range of conditions tolerated by *M. arenaria* (see Materials and Methods). If temperature and salinity differences did occur, their effects would be minimal.

Substrate differences at the Stonington and Westport sites appear to be the most immediate cause of the observed differences in age-specific fecundity and survivorship. Several investigators have found that sediment type is important in controlling growth rate and shell allometry in *M. arenaria* (Belding 1930; Swan 1952; Newell and Hidu 1982). Clams grown on coarse sediments (gravel, cobble), such as that at the Westport site are slow-growing and more globose in shape than clams from sand or mud environments. Although differences in growth rate could be due to differences in food availability at the two sites, the allometric variations (Brousseau and Baglivo 1987) strongly support the hypothesis that substrate effect is the factor controlling growth. Reduced body size in Westport clams may have an indirect effect on fecundity by restricting egg production. In addition, both Glude (1954) and Pfitzenmeyer and Drobeck (1967) demonstrated that *M. arenaria* burrows fastest in fine-grained sediments since physical resistance to burrowing increases with increasing particle size (Trueman 1954). Hence, the high daily maintenance requirements of Westport clams may result in less energy available for reproduction, long-term maintenance, and survival. The Westport population may be an example of a population inhabiting a marginal environment.

The underlying pattern of life history (reproductive effort, patterns of recruitment, survival profile, and growth schedule) for both populations of *M. arenaria* is very similar. This is not surprising since population parameters are viewed as evolved, species-specific traits. Nevertheless, our evidence for local differentiation in different habitats demonstrates the degree to which individual populations of a widespread species can respond in different ways to their immediate environments; environmental heterogeneity can be reflected in the structures and dynamics of local populations.

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APPENDIX

APPENDIX TABLE 1.—Empirical distributions for age-size relationships for the Westport, CT *Mya arenaria* population. Percentage in each size category per age are indicated in parentheses.

Size (mm)	Age (yr)								
	1	2	3	4	5	6	7	8	9+
10–20	1 (3.8)								
20–30	9 (34.6)	3 (2.0)							
30–40	13 (50.0)	55 (37.2)	19 (12.7)	2 (2.9)					
40–50	3 (11.5)	70 (47.3)	65 (43.3)	15 (21.4)	7 (15.6)	4 (8.7)	3 (8.3)	3 (7.9)	
50–60		19 (12.8)	60 (40.0)	40 (57.1)	24 (53.3)	23 (50.0)	16 (44.4)	17 (44.7)	6 (23.1)
60–70		1 (0.7)	5 (3.3)	12 (17.1)	13 (28.9)	17 (37.0)	14 (38.9)	14 (36.8)	14 (53.8)
70–80				1 (1.4)	1 (2.2)	2 (4.3)	2 (5.6)	4 (10.5)	6 (23.1)
80–90							1 (2.8)		

APPENDIX TABLE 2.—Empirical distributions for age-size relationships in the Stonington, CT *Mya arenaria* population. Percentage in each size category per age are indicated in parentheses.

Size (mm)	Age (yr)					
	1	2	3	4	5	6+
20–30	15 (26.8)					
30–40	22 (39.3)	4 (5.1)				
40–50	13 (23.2)	5 (6.4)	2 (1.1)			
50–60	6 (10.7)	31 (39.7)	37 (20.2)	5 (3.8)		1 (7.1)
60–70		31 (39.7)	94 (51.4)	26 (19.8)	2 (7.1)	1 (7.1)
70–80		7 (9.0)	41 (22.4)	66 (50.4)	14 (50.0)	4 (28.6)
80–90			9 (4.9)	31 (23.7)	11 (39.3)	6 (42.9)
90–100				3 (2.3)	1 (3.6)	2 (14.3)

A LONG-TERM STUDY OF "MICROCELL" DISEASE IN OYSTERS WITH A DESCRIPTION OF A NEW GENUS, *MIKROCYTOS* (G. N.), AND TWO NEW SPECIES, *MIKROCYTOS MACKINI* (SP. N.) AND *MIKROCYTOS ROUGHLEYI* (SP. N.)

C. AUSTIN FARLEY,[1] PETER H. WOLF,[2] AND RALPH A. ELSTON[3]

ABSTRACT

Continuing long-term studies of oyster disease problems have been carried out over the past 26 years using field monitoring, gross, histologic, and ultrastructural pathologic methods.

A microorganism of uncertain taxonomy was discovered in 1963 by J. G. Mackin in association with lesions and mortalities of Japanese oysters, *Crassostrea gigas*, from Denman Island, British Columbia, Canada. Mackin coined the term "microcell" for this organism and described the parasite as 1–3 μm cells with small nuclei which occurred within vesicular connective tissue cells adjacent to characteristic abscesses. We are describing this organism as *Mikrocytos mackini* sp. n. in his honor. Similar appearing organisms were seen by the senior author in flat oysters, *Ostrea edulis*, from Milford, Connecticut, on three different occasions: 1) in oysters transferred from Milford, Connecticut, to Chincoteague Bay, Virginia; 2) in oysters transferred from Milford to Elkhorn Slough, California; and 3) in oysters transferred from Milford to Oxford, Maryland, and held in recirculated sea water. The causative organism in these three episodes has been shown by electron microscopy to be *Bonamia ostreae*, the parasite that was implicated in recent mortalities in flat oysters in Europe. Similar organisms have also been seen in Olympia oysters, *Ostrea lurida*, from Oregon and in the Sydney rock oyster, *Saccostrea commercialis*, from Australia. Presence of the organism in the latter species is associated with the winter mortalities originally described by T. C. Roughley, and the pathogen is here described as *Mikrocytos roughleyi* (sp. n.) in his honor.

"Microcell" type parasites of oysters are associated with a complex of diseases that occur in Japanese oyster, *Crassostrea gigas*; Sydney rock oyster, *Saccostrea commercialis*; flat oyster, *Ostrea edulis*; and Olympia oyster, *O. lurida*, in North America, Europe, and Australia. Severity of disease varies from an acute, highly lethal form to a chronic, seasonally recurring disease that does not produce massive mortalities. The etiologic agents are small, morphologically simple, and very difficult to compare and characterize taxonomically at light microscope levels of resolution. Associated lesions vary according to species affected and provide some of the differences that may be used to distinguish the agents involved. The complexity of this group and the difficulties involved in achieving an understanding regarding whether we are dealing with one or a group of organisms and how they were transferred to new locations, the long time span involved in answering these questions, and the continuing dissemination of unpublished privileged information shared in informal workshop gatherings of scientists with common interests, make it necessary to use unpublished anecdotal information in order to provide as complete a story as possible.

The first oyster mortality known to be associated with "microcell" disease was reported in *C. gigas* from Denman Island, British Columbia, Canada by Quayle (1961). Quayle's report documents the epizootic aspects from 1956 to 1960 and demonstrates the gross appearance of the disease in the Pacific oyster. A causative agent was not identified until several years later, when the late J. G. Mackin[4] (unpubl. data) discovered a small intracellular organism intimately associated histologically with tissue abscesses in diseased oysters (*C. gigas*) from Denman Island and called this organism "microcell". He demonstrated this material at the 1963 Shellfish Mortality Conference held at Oxford, MD.

Mackin's demonstration provided us with the insight to identify similar organisms in histologic sec-

[1]Northeast Fisheries Center Oxford Laboratory, National Marine Fisheries Service, NOAA, Oxford, MD 21654.
[2]62 MacKenzie Street, Bondi Junction, New South Wales, Australia 2022.
[3]Center for Marine Disease Control, Battelle/Marine Research Laboratory, Sequim, WA 93282.

[4]J. G. Mackin, deceased, Texas A&M University, College Station, TX.

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tions of Denman Island oysters in our laboratory collection and further led to the discovery of microcell disease in *O. edulis*, *O. lurida*, and *S. commercialis* from Australia ("Australian winter disease") described by Roughley (1926). In 1979, the characteristics of microcell disease were demonstrated at a microscopic diagnosis workshop held at the Ministry of Agriculture and Fisheries Laboratory in Weymouth, England. This workshop was attended by molluscan pathologists from several European countries including France. In the late 1970s, serious mortalities of *O. edulis* in France, associated with microcell infections, were described in a paper by Pichot et al. (1979), in which the organism was named *Bonamia ostreae*. Reference to the earlier work on microcell by Mackin and others (Katkansky et al. 1969) was not included in their report.

Since the taxonomic relationship and status of these similar parasites have not been described, it is the purpose of this paper to present a complete background on microcell related epizootics and morphological information which, in North America, preceded the French report (Pichot et al. 1979). Furthermore, microscopic and ultrastructural comparisons of the microorganisms are provided and a new genus, *Mikrocytos* g. n., and two new species, *Mikrocytos mackini* sp. n. and *Mikrocytos roughleyi* sp. n., are described.

MATERIALS AND METHODS

General Procedures

Oyster tissues were collected from a variety of sources as follows:

Code WWC were *C. gigas* collected from Henry Bay, Denman Island, British Columbia, Canada on a periodic basis from April 1968 to June 1969 by D. B. Quayle (spring 1969 samples were collected by N. Bourne). Live oysters were sent by air freight to the Oxford Laboratory where clinical and gross features were recorded and they were processed for histological and, in some cases, ultrastructural studies.

Code S-124-A were *C. gigas* from Hawaii collected in September 1972.

Code S-41 were *S. commercialis* collected by Peter Wolf from 22 July to 23 July 1965 from the Georges River, Woolooware Bay, New South Wales and shipped to the Oxford Laboratory for processing.

Code FK were progeny of *O. edulis* from Boothbay Harbor, ME that were spawned at Milford, CT in April 1961. Seed oysters were transplanted to Chincoteague Bay, VA in May 1961 and processed at subsequent intervals (FK-1-1 to FK-2-5, August 1961; FK-3-1, August 1961; FK-4-1 and FK-4-2, February 1962).

Code WAC were *O. edulis* bred in the Milford, CT hatchery from 1963 to 1965, and introduced into California bays as follows:

WAC-1, Milford 1963 seed oysters planted in Morro Bay, CA in December 1964 and sampled on 7 December 1965 during a heavy mortality.

Sample WAC-21-28 consisted of 38 oysters from a Milford 1963 stock shipped to California in 1964 and held at Pigeon Point Laboratory, Pigeon Point, CA until heavy mortality occurred and sampled on 11 May 1966.

WAC-3-1-10 were 1963 Milford oysters placed in Morro Bay in 1964. Heavy mortality was noted and samples were taken. WAC-3-11-15 were 1963 Milford stock placed in Morro Bay in 1964. Mortality was low. Oysters were necropsied and fixed on 1 May 1966. WAC-3-16-26 were Milford 1962 stock placed in Morro Bay in 1963. They experienced 40% mortality and were examined and fixed on 1 May 1966. Oysters WAC-4-1 through 4-5 were from Milford 1963 stock placed in Tomales Bay, CA in 1964; low mortality was observed. They were examined and fixed on 1 May 1966.

Code FMT were *O. edulis* used in an experimental holding study at the Oxford Laboratory. Ten 2-yr-old *O. edulis* from the Milford hatchery were placed in each of three tanks receiving 0.45 μm membrane filtered 26‰ seawater on 23 February 1968; pH, temperature, salinity, and mortality were monitored daily until 10 October 1968. *Crassostrea virginica* from the Mispillian River, Delaware Bay, were placed in each tank on 28 March. Tanks were designated A (control), B (fed tissues of moribund *O. edulis* from Pigeon Point, CA), and C (fed tissues from Denman Island *C. gigas* infected with Denman Island disease). Seawater in each tank was recirculated through a glass wool, charcoal, calcium flow-through filter via an airlift system moving from C to B to A, respectively. Oyster codes were FMT-A-1-20, FMT-B-1-20, FMT-C-1-20, numbered as they were fixed (species were designated at time of fixation).

Code WAO-A were 50 specimen samples of native oysters (*O. lurida*) from Yaquina Bay, OR, sampled

monthly from February 1969 to January 1971. Samples were coded from WAO-7A to WAO-22A.

Tissues were fixed in Zenker's acetic, Davidson's fluid (Shaw and Battle 1957), or McDowell's fixative (McDowell and Trump 1976) as modified by Farley et al. (1986) (1% glutaraldehyde/4% formaldehyde; pH 7.2–7.4 in one-half ambient seawater). Six μm sections were stained with Harris' hematoxylin-eosin, Ziehl's fuchsin, periodic acid Schiff reagent (PAS) with malt diastase digestion, Feulgen picromethyl blue (Farley 1969), or Giemsa (Howard and Smith 1983).

Electron Microscopy Procedures

Lesions from *C. gigas* from Denman Island were fixed in 2% glutaraldehyde in pH 7.2 seawater, postfixed in 1% osmium tetroxide in phosphate buffer, pH 7.2, and embedded in Epon-Araldite (Feng et al. 1971). Fifty to 100 nm sections, selected on the basis of interference color (silver), were cut and stained with lead citrate and uranyl acetate. *Ostrea edulis* sections from the WAC material (WAC-2-19) were deparaffinized, postfixed in 2% glutaraldehyde and 1% osmium tetroxide, plastic embedded, ultrasectioned, and stained in the same fashion as the *C. gigas* materials. Sections were examined in a Zeiss[5] EM 9 electron microscope.

RESULTS

"Denman Island Disease" Studies

Table 1 presents the seasonal prevalence of gross features of samples collected in this study. Visual condition index remained high (most oysters in medium to fat condition). Mantle recession occurred most commonly from April through June and was most prevalent in June. Pale digestive gland was present in up to 24% of the oysters in the spring and was also seen in up to 16% of the oysters in fall samples. Shell pustules (Fig. 1), abscesses, and ulcers as described by Quayle (1961) (Fig. 2) were present from April through June.

Microscopical examination (Table 2) revealed granular hemocyte infiltration of vesicular connective tissue (VCT) in most samples with high prevalences of microcell infections occurring sporadically throughout the years. Abscesses (Fig. 3) in the VCT of the mantle and gonad consisted of apparently viable granular hemocytes at the periphery with phagocytosis of moribund cells deeper in the lesion and coagulative necrosis in the center. Microcell organisms were associated with these abscesses. The parasite (Fig. 4) was 1–3 μm in diameter, contained a small (1 μm) Feulgen-positive nucleus, and occurred cytozoically in VCT cells and extracellularly adjacent to and within abscesses. Microcells occurred in 60% of the abscesses found in histologic sections. However, microcells were never found outside of abscesses.

A similar disease was discovered by F. Kern[6] in *C. gigas* from Hawaii. Microcell parasites were similar in morphology and size (Figs. 5, 6) to the Denman Island organism, but infections were more

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[6]F. G. Kern, Northeast Fisheries Center Oxford Laboratory, National Marine Fisheries Service, NOAA, Oxford, MD 21654, pers. commun.

TABLE 1.—Gross pathology in oysters from Denman Island, B.C.

Code	Date	Number in sample	% fat condition	% medium condition	% watery condition	% mantle recession	% pale digestive gland	% shell pustules	% with abscesses
WWC-1	22 May 1967	27	88	11	0	11	0	7	7
WWC-2	5 June 1967	28	100	0	0	11	7	14	7
WWC-3	10 Apr. 1968	25	88	4	8	78	24	0	16
WWC-4	22 Apr. 1968	25	100	0	0	28	0	4	12
WWC-5	24 May 1968	25	100	0	0	0	0	0	4
WWC-6	24 June 1968	25	92	8	0	8	0	4	0
WWC-7	5 Aug. 1968	25	48	48	7	8	0	0	0
WWC-8	14 Oct. 1968	25	100	0	0	0	0	0	0
WWC-9	18 Nov. 1968	25	76	24	0	0	16	0	0
WWC-10	27 Jan. 1969	25	44	56	0	0	4	0	0
WWC-11	26 Feb. 1969	18	33	61	6	0	0	0	0
WWC-12	21 Mar. 1969	25	96	7	0	0	0	0	0
WWC-13	11 Apr. 1969	25	100		0	0	4	16	16
WWC-14	12 May 1969	25	72	28	0	0	0	12	12
WWC-15	20 June 1969	25	88	12	0	12	0	4	0
WWC-18	9 June 1980	42	95	2	2	19	0	17	17

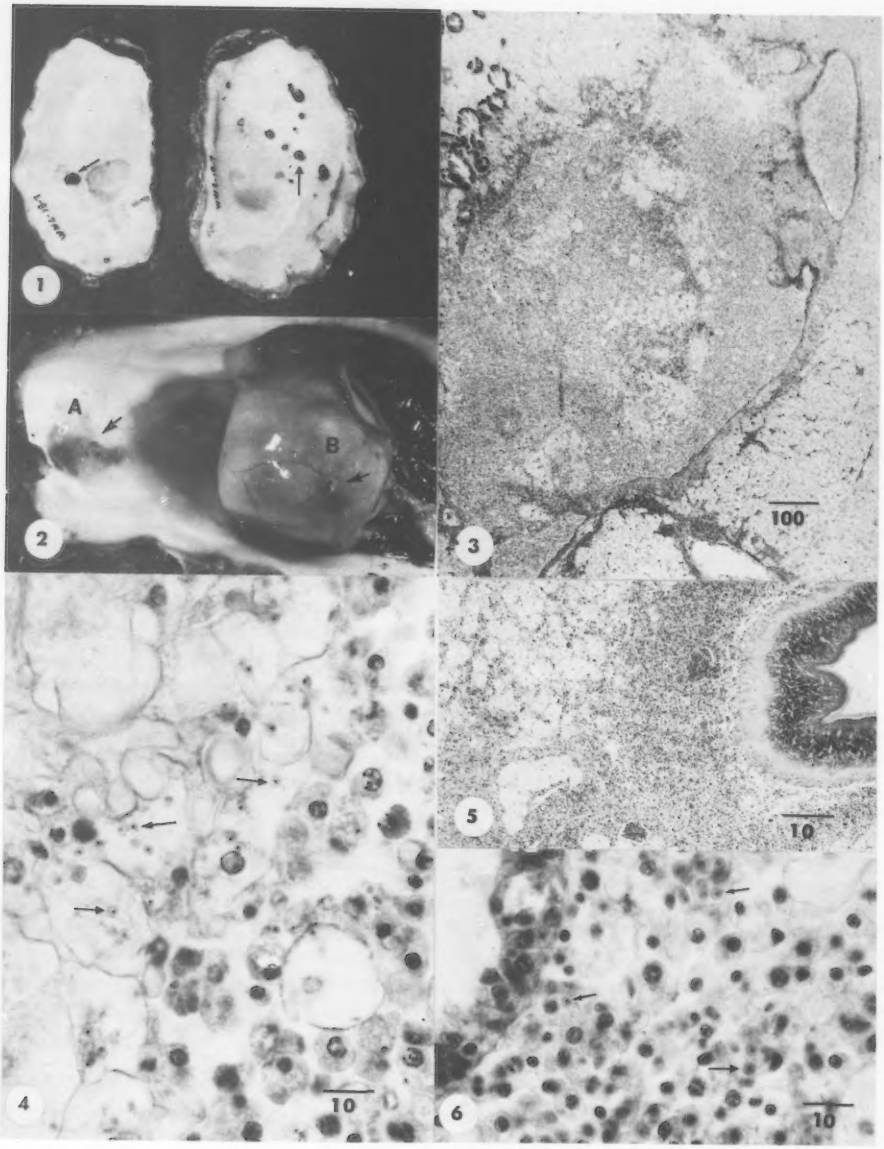

1
A
B
2
3
100
4
10
5
10
6
10

TABLE 2.—Percentage of prevalance of lesions and parasites in Denman Island oysters.

Code	Date	Granulocyte infiltration (%)	Tissue abscess (%)	Hyaline hemocyte infiltration (%)	Neoplasms (%)	Microcell infection (%)	Mytilicola (%)	Ciliates	
								Gill (%)	Other (%)
WWC-1	22 May 1967	33	7	0	0	7	7	4	4
WWC-2	5 June1967	4	18	0	0	14	4	4	0
WWC-3	10 Apr. 1968	40	16	0	0	4	0	0	0
WWC-4	22 Apr. 1968	0	16	0	0	16	0	0	4
WWC-4	24 May 1968	8	4	0	0	4	0	0	4
WWC-6	24 June1968	32	4	24	0	0	0	0	0
WWC-7	5 Aug. 1968	0	0	0	0	0	0	0	0
WWC-8	14 Oct. 1968	36	0	0	4	0	0	0	0
WWC-9	18 Nov. 1968	12	7	36	8	0	0	0	0
WWC-10	27 Jan. 1979	20	0	8	0	0	0	0	0
WWC-11	26 Feb. 1969	4	0	0	0	0	0	0	0
WWC-12	21 Mar. 1969	8	4	0	0	4	8	0	0
WWC-13	11 Apr. 1969	20	20	8	0	12	0	4	4
WWC-14	12 May 1969	24	32	0	8	16	0	0	0
WWC-15	30 June1969	8	12	0	0	0	0	0	0
WWC-18	9 June1980	4	20	0	0	16	8	0	0

systemic with diffuse inflammatory infiltration of connective tissue (Fig. 5) associated with the presence of microcell parasites (Fig. 6). Microcells were cytozoic in hemocytes and VCT. Focal abscesses were present but not nearly as prominent in the Hawaiian oysters as the lesions in Denman Island oysters.

Australian Winter Disease Studies in *Saccostrea commercialis*

Australian winter disease was characterized by pustules, ulcerations, and abscesses (Fig. 7). Seven individuals, consisting of six females and one male, displayed ulcerations in the gonad and mantle. Ulcerations of the gills were also common and frequently occurred near the adductor muscle. Impaired adductor muscle contraction was characteristic of the disease.

Histologically, the animals contained abscesses (Fig. 8) with intense phagocytic infiltrations in the connective tissue and varying degrees of necrosis. The abscesses contained a small (1–2 μm) organism (Figs. 9, 10) which contained a nucleus >1 μm that was spherical with bipolar or eccentric nucleolar structures. The size and cytozoic location of these organisms suggest a strong similarity to other microcell type parasites seen in other species of oysters. Four of the six females had gonads in a state of resorption and digestive diverticular epithelium was slightly metaplastic in two of the seven oysters.

Microcell Disease Study in *Ostrea edulis*

Episode 1

Microcell disease in *O. edulis* from progeny from Boothbay Harbor, ME brood stock spawned at Milford, CT and transferred to Chincoteague Bay, MD (Code FK).

Two of the 13 oysters fixed between August 1961 and July 1962 had heavy infection of microcells (Fig. 13) which were 1–3 μm in diameter with a Feulgen-positive nucleus (1 μm diameter) and found intracellularly within hemocytes. In three of the other oysters, moderate infiltrations of hemocytes were observed but without parasites.

FIGURE 1.—Right and left valves of *Crassostrea gigas* from Denman Island, British Columbia. The darker rounded lesions are conchiolinous shell pustules characteristic of the Denman Island disease.

FIGURE 2.—Scale units in Figures 2–15 are in micrometers. Macrophotograph showing shell pustule (A) and adjacent tissue ulcer (B).

FIGURE 3.—Histologic section from Denman Island oyster. A large abscess-type lesion is apparent in the connective tissue-gonad region of the section. 100×. Feulgen picromethyl blue (FPM) stain (specimen WWC-2-7).

FIGURE 4.—Higher magnification photomicrograph taken at the edge of the lesion in Figure 3. Many microcell protistan parasites (*Mikrocytos mackini* sp. n.) are evident in vesicular connective tissue cells adjacent to necrotic inflammatory cells deeper in the lesion. 1,000×. Harris' hematoxylin and eosin (HHE) stain (specimen WWC-2-7).

FIGURE 5.—Lesion caused by microcell infection in *C. gigas* from Hawaii. 100×. HHE stain (specimen S-124A-45).

FIGURE 6.—High magnification photomicrograph showing microcell parasites intracellular in hemocytes in vesicular connective tissue of the Hawaiian oyster. 1,000×. HHE stain (specimen S-124A-45).

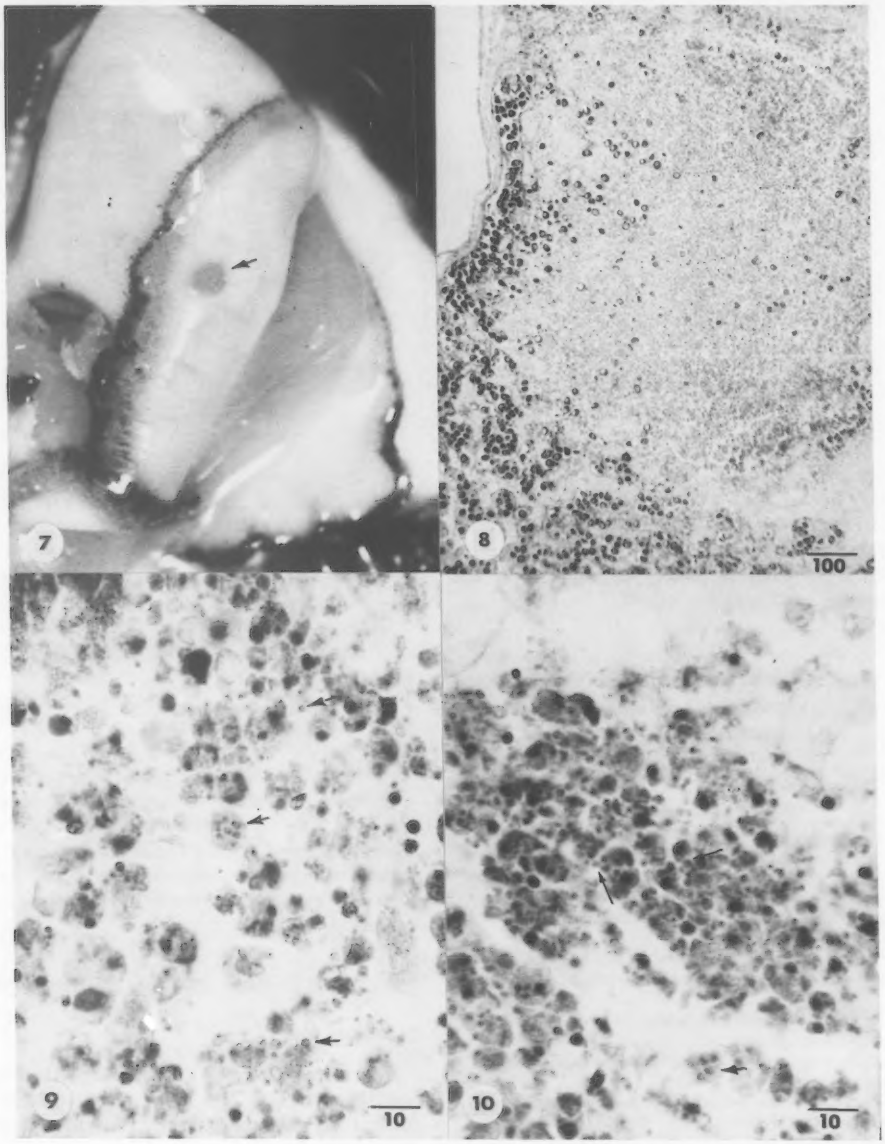


FIGURE 7.—Ulceration in the mantle of *Saccostrea commercialis* with Australian winter disease.

FIGURE 8.—Large abscess-type lesion in the connective tissue-gonad region of *Saccostrea commercialis* (code S-41-7) from Australia with Australian winter disease. 100×. HHE stain (specimen S-41-7).

FIGURE 9.—Higher magnification photomicrograph from lesion in Figure 8. Note intracellular microcell parasites (*Mikrocytos roughleyi* sp. n.) with hemocytes. 1,000×. HHE stain (specimen S-41-7).

FIGURE 10.—Heavy infection of Australian winter disease; microcell parasites in the gonad of S-41-4. 1,000×. HHE stain.

Episode 2

Microcell disease in *O. edulis* transferred from Milford, CT to Elkhorn Slough, CA (Code WAC).

Epizootiological gross and histopathologic data are presented in Table 3. Clear association is apparent between high mortality, emaciation (watery condition), mantle recession, hemocytic infiltration, and heavy microcell infection.

Infections were particularly intense in gill and GI tract epithelia which contained dense infiltrations of infected hemocytes (Fig. 11). Infections were characterized by the intracellular (in hemocytes) and extracellular presence of "microcell" organisms (Fig. 12) similar to those seen in the Chincoteague Bay (FK) samples.

Episode 3

Microcell disease in *O. edulis* transferred from Milford, CT to aquaria in Oxford, MD (Code FMT).

The experiment ran from 20 February 1968 until 9 October 1968. No transmission was noted. However, tank C drained accidentally on 19 March and the filtered seawater was replaced with unfiltered seawater from Chincoteague Bay, VA. A combined total of 9 of 11 animals died between 22 March and 27 March and the remaining 2 live oysters were fixed on 28 March.

The first six that died were from tank C and had moderate to heavy cases of microcell disease with associated hemocytic infiltration. Histologic examination of both species, either after mortalities, or when they were sacrificed in October, failed to reveal any more infections. The parasites and disease characteristics were identical to the previously described cases (Fig. 14).

Microcell Disease Study in *Ostrea lurida*

Microcell disease in *O. lurida* from Yaquina Bay, OR (Codes WAO-7-A and WAO-12-A).

Monthly to bimonthly samples of 50 specimens were examined grossly and for histopathology for a 2-yr period. A 24% prevalence of microcell disease was seen in WAO-7-A samples collected in February 1969, and 12% prevalence was seen in the WAO-12-A samples collected in February 1970. No microcell infections were seen in any of the other samples. However, neoplasms and *Mytilicola orientalis* infections were seen commonly throughout the study.

Microcell infections tended to be less intense than in *O. edulis*, but organisms were similar in size and appearance to the organisms seen in flat oysters (Fig. 15). Intracellular infections were in VCT cells and not hemocytes.

Ultrastructural Studies

Electron microscopy revealed *O. edulis* parasites that were usually intracellular with up to three organisms per cell. Parasites were 1–3 μm in diameter, and contained an eukaryotic nucleus about 1 μm in diameter. A crescent-shaped, peripheral nucleolus was evident in most organisms (Fig. 16). The cytoplasm contained numerous ribosome-like organelles and spherical dense bodies, presumably membrane bound, which were 90–130 nm in diameter, and generally resembled the "haplosporosomes" (Fig. 17) described in other haplosporidan

TABLE 3.—Epizootiology of microcell disease in *O. edulis* from California.

Code	Stock origin	Sample location	Date fixed	Mortality	*N*	Condition			Mantle recession	Hemocyte infiltration	Microcell infection
						Fat	Med	Watery			
WAC-1 (1–20)	Milford 1964	Morro Bay	7 Dec. 1965	Heavy	20	no gross data				18	18
WAC-2 (1–25)	Milford 1964	Pigeon Pt.	1 May 1966	Heavy	38	1	8	19	22	25	25
WAC-3 (1–10)	Milford 1964	Morro Bay	1 May 1966	Heavy	10	2	6	2	6	8	8
WAC-3 (11–15)	Milford 1963	Morro Bay	1 May 1966	Low	5	4	1	0	0	0	0
WAC-3 (16–26)	Milford 1963	Morro Bay	1 May 1966	40%	10	6	4	0	1	6	3
WAC-3 (27–31)	Milford 1965	Morro Bay	1 May 1966	0	5	5	0	0	0	0	0
WAC-4 (1–5)	Milford 1964	Tomales Bay	1 May 1966	Low	5	5	0	0	1	0	0

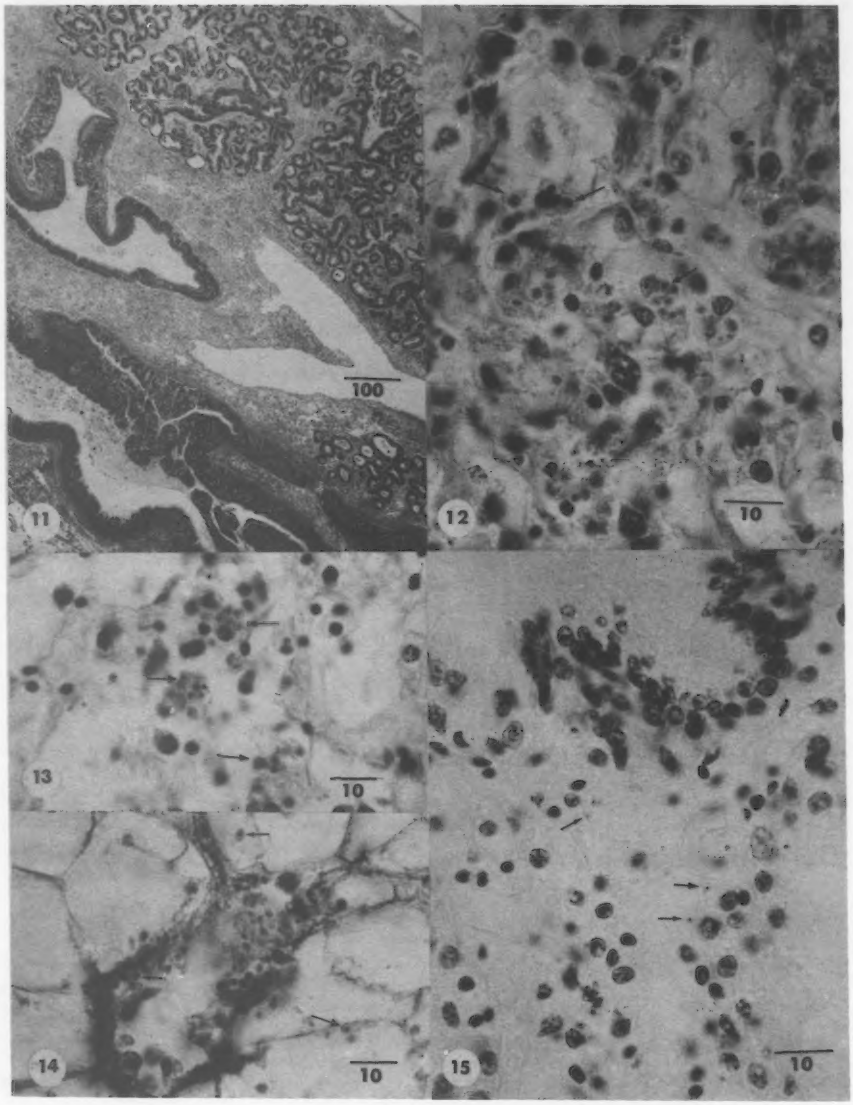


FIGURE 11.—Low magnification view of *Ostrea edulis* from California (WAC-2-29). Note diffuse inflammatory infiltrate in vesicular connective tissue. 100×. HHE stain.

FIGURE 12.—Microcell infection in *Ostrea edulis* (specimen WAC-2-19) from population of oysters introduced into California waters from Milford, CT. 1,000×. HHE stain.

FIGURE 13.—Microcell infection in hemocytes in *Ostrea edulis* transported from Milford, CT to Chincoteague Bay, VA in 1962 (first diagnosed case of *Bonamia ostreae*). 1,000×. HHE stain (specimen FK-5-1).

FIGURE 14.—Microcell infection in *Ostrea edulis*. Transferred from Milford, CT to Oxford, MD recirculated seawater aquarium. Cells of the vesicular connective tissue are infected. 100×. HHE stain (specimen FMT-B-1-3).

FIGURE 15.—Microcell infection in vesicular connective tissue and hemocytes of *Ostrea lurida* from Yaquina Bay, OR. 1,000×. FPM stain (specimen WAO-7A-41).

parasites (Perkins 1979). Larger "membrane" bound structures (500 nm) consistent with the appearance of mitochondria were also present in the cytoplasm; however, cristi could not be distinguished.

Ultrastructural studies were also performed on positively diagnosed oysters (*C. gigas*) from Denman Island, British Columbia (sample WWC-18, collected 9 June 1980). Microcells were always associated with focal abscesses, but their occurrence was restricted to the periphery. Parasites were found as cytozoic organisms primarily in VCT cells (Fig. 18). Microcells were 3–4 μm in diameter, had nuclei 1 μm in diameter, and nucleoli 250–300 nm in diameter. Nucleoli were spherical, eccentrically located within the nucleus, but never peripheral (Fig. 19). One to many parasites occurred within the cytoplasm of vesicular cells. None were ever found within hemocytes. Figure 20 shows an organism possibly undergoing division. The cytoplasm was densely packed with free ribosomes and contained a variety of organelles as follows: double membrane bound dense bodies 50–185 nm in diameter (Fig. 19A); double membrane bound, dumbbell-shaped structures (Figs. 20, 21h), approximately 37 × 18 nm to 85 × 260 nm; and dense bodies 40–45 nm in diameter that appeared to be membrane bound, and a suggestion of six- and five-side angularity (Figs. 19, 20, 21v). Endoplasmic reticulum was extremely sparse if present at all. The plasma membrane complex consisted of possibly two membranes with the external membrane containing dense material. An electron-lucent zone was present around the cell, suggestive of a glycocalyx.

Taxonomic Descriptions

The information acquired on these diseases and the organisms associated with them and outlined previously allows us to propose taxonomic descriptions of them.

Mikrocytos g. n. (*Protista incerta sedis*) (little cell)— Definitive life cycle stages that would permit higher classification of this protistan parasite have not been observed. Named after the term microcell as coined by the late John G. Mackin. Small (1–4 μm), unicellular, protistan, cytozoic parasite normally infecting VCT cells of oysters. Always associated with abscess-type focal inflammatory lesions.

Type species - *Mikrocytos mackini* sp. n.

Bonamia, the other closely similar genus, infects hemocytes of ostreid oysters only and is associated with systemic non-abscess type disease manifestations.

Mikrocytos mackini sp. n. — Named in honor of the late John G. Mackin who discovered this parasite in the early 1960s.

Type specimen - A 6 μm thick hematoxylin-and-eosin-stained histologic section of an infected oyster, *C. gigas* (WWC-2-7), was deposited in the Registry of Marine Pathology, Northeast Fisheries Center, Oxford, MD 21654.

Host - *Crassostrea gigas*

Type locale - Henry Bay, Denman Island, British Columbia, Canada.

Range - Occurrence confined to above site. (A closely related candidate for inclusion within this species was found in *C. gigas* from Hawaii.)

Morphologic characteristics - Small, 1–4 μm intracellular parasites of VCT cells; infections always associated with focal inflammatory tissue abscesses. Parasites are unicellular and contain a small 1 μm nucleus that has an eccentric nucleolus 250–300 nm in diameter. The cytoplasm contains dense, double membrane bound, dumbbell-shaped haplosporosome-type organelles 50–180 nm in diameter and 40–45 nm membrane bound five- and/or six-sided dense bodies.

Mikrocytos roughleyi sp. n. — Named in honor of T. C. Roughley who published the initial study of the Australian winter disease in the 1920s.

Type specimen - A 6 μm thick hematoxylin-and-eosin-stained section of an infected oyster, *S. commercialis* (S-41-7), was deposited in the Registry of Marine Pathology, Northeast Fisheries Center, Oxford, MD 21654.

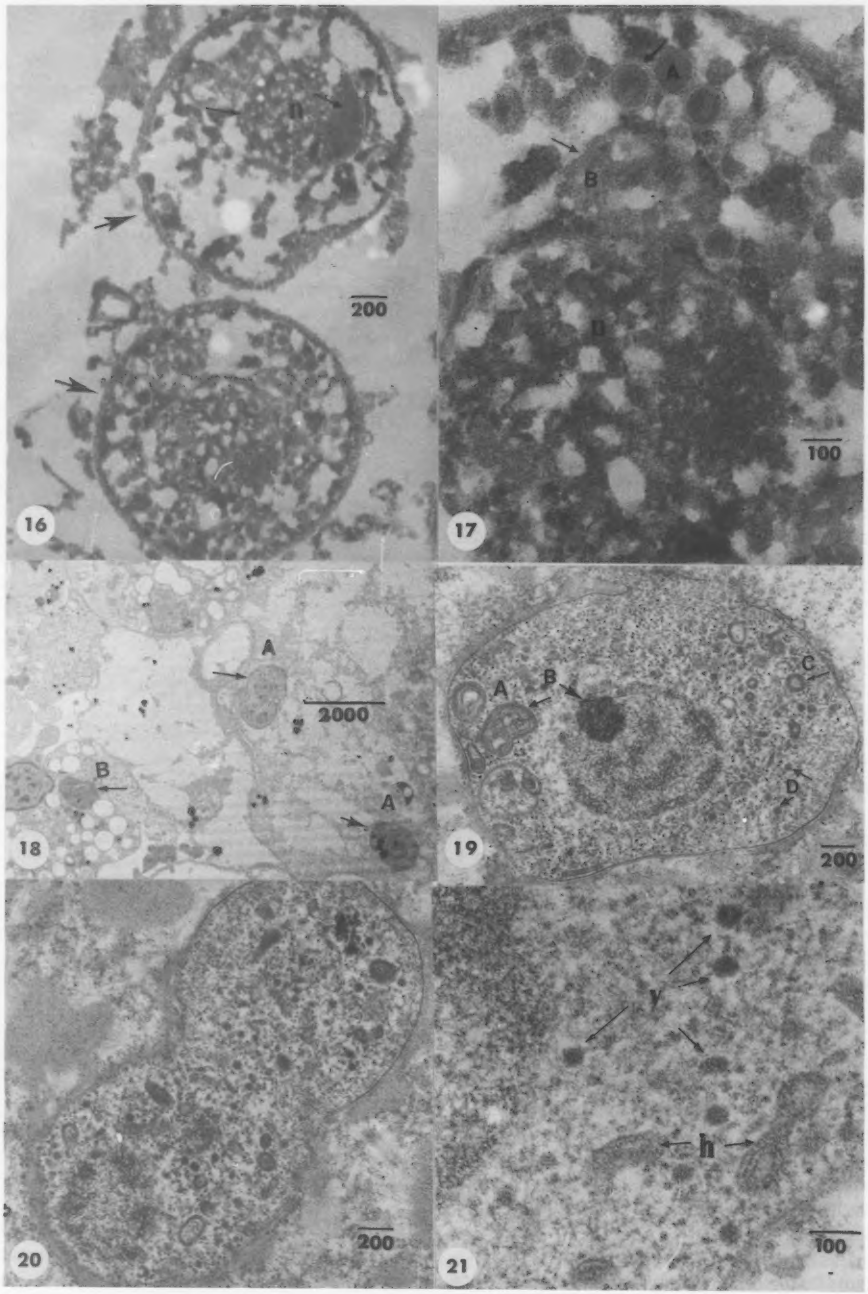
Host - *Saccostrea commercialis*

Type locale - Georges River, Woolooware Bay, New South Wales, Australia.

Range - Known only from the above location and other high salinity estuaries in this region of New South Wales.

Morphologic characteristics - Infections occur in hemocytes and are associated with focal abscess-type lesions in the gill, connective, and gonadal tissues. Organisms are small 1–3 μm cells that contain an eccentric nucleus and a cytoplasmic vacuole. Ultrastructural characteristics are not known.

Comparisons — *Mikrocytos* g. n. is always associated with focal abscesses and occurs in crassostreid oysters. *Bonamia* is always associated with generalized infections and only occurs in ostreid oysters.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Mikrocytos mackini sp. n., which has eccentric nucleoli, and *M. roughleyi* sp. n., which has a cytoplasmic vacuole and a nucleus that is displaced to the periphery of the cell, are morphologically distinct from *B. ostreae* (the only closely related species). All three species occur in separate host species and all appear to be host specific.

DISCUSSION

Denman Island Disease

Quayle's original study (1961) documented heavy mortality (40%) clearly associated with surface tissue pustules in *C. gigas* in an area of British Columbia in May. Studies of *C. gigas* by Mackin resulted in the discovery of the "microcell" organism and its association with tissue abscesses. Subsequent histological examinations done by the senior author, in cooperation with D. Quayle and N. Bourne, confirmed the association of mortality, pustules, tissue abscesses, and microcell infections that have continued to occur during each May and June to the present time.

Histopathologically, this disease (caused by *Mikrocytos mackini*) is characterized by acute inflammatory abscesses which remain focal until the oyster dies or resolution occurs. While microcell organisms are not always found in abscesses, they are never found in oysters that do not have abscesses, indicating at least an associational relationship.

Electron microscopy has demonstrated only one stage of a small protistan organism that contains organelles resembling haplosporosomes. No clear demonstration of mitochondria has been accomplished. The haplosporosome-like organelles often tend to be elongated and contain layers of membranes. Internal structure of these organelles is not nearly as dense as that seen in *Bonamia* or other haplosporidans.

The small 45 nm dense bodies also seen in the cytoplasm have characteristics suggestive of virus structure; namely, uniform size, abundant occurrence in the cytoplasm only, and a suggestion of icosahedral symmetry. The cytoplasmic occurrence, 46 nm size, icosahedral symmetry, and the presence of an envelope are characteristics of the family Togaviridae. The lack of paracrystalline arrays, strategy of development, empty capsids, and extracellular occurrence prevent conclusive identification of these particles as virus at this time, and these may prove to be an exclusive organelle that is a characteristic of this protistan group. The presence of a lytic virus in the parasite could also explain the self-limiting nature of the focal abscesses characteristic of the Denman Island disease.

Australian Winter Disease

Since Roughley described this disease in an Australian *S. commercialis* in 1926, little progress has been made toward identification of the etiologic agent. Careful examination of the tissues of affected animals, collected by Peter Wolf, has revealed apparent small cytologic and histozoic organisms associated with abscesses. These organisms have features such as size, morphology, and tissue location remarkably similar to organisms present in other oyster microcell diseases. Peter Wolf (unpubl. data) has stated that this disease thrives in high (30–35‰) salinity (and is unknown in lower salinities); the incubation period is about 2½ months and mortality does not occur in animals less than 3 years old. The occurrence of shell lesions and focal tissue abscesses appears to be common features in *Saccostrea* and *Crassostrea*. This may indicate a degree of resistance characterized by the ability of the animal to isolate parasites in a focal lesion and to eliminate them by either rupture of the abscesses or diapedesis through the mantle epithelium to the shell surface, with subsequent calcification via shell pustule formation, or it may indicate a host parasite relationship response. This mechanism was reported in oysters that had acquired resistance to *Haplosporidium nelsoni* (Farley 1968).

Kern (fn. 6) found microcell infections in *C. gigas* from Hawaii (Fig. 6) that were not always associated with focal abscesses. General systemic infection and inflammatory infiltration were noted in these cases (Fig. 5), but the organisms appear

FIGURE 16.—Scale units in Figures 16–21 are in nanometers. Electron micrograph of deparaffinized *Ostrea edulis* from California. Two intracellular microcells showing prominent nuclei with peripheral nucleoli. 36,000×.

FIGURE 17.—Higher magnification of California microcells showing haplosporosome-like bodies (A) and a probable mitochondria (B). 108,000×.

FIGURE 18.—Electron micrograph of several microcells in vesicular connective tissue of *Crassostrea gigas* (A) from Denman Island, British Columbia. Probable degenerate microcells can also be seen in the cytoplasm of phagocytic hemocytes (B). 7,320×.

FIGURE 19.—Electron "micrograph" of microcell from Denman Island *Crassostrea gigas*. Note the eccentric nucleolus (A), myelin bodies (B), haplosporosome-like bodies (C), and virus-like entities (D). 36,900×.

FIGURE 20.—Electron micrograph of *Crassostrea gigas* microcell with structure suggestive of division. 36,900×.

FIGURE 21.—Higher magnification of electron micrograph showing haplosporosomes and virus-like dense bodies. 108,000×.

to be identical to the Denman Island microcell organisms.

Microcell Infections in *Ostrea edulis*

Microcell infections were first seen in *O. edulis* in moribund oysters which had been transferred from Milford, CT to Chincoteague Bay, VA in 1962. Two animals from the FK sample had developed clinical manifestations of the disease. Other cases appeared in animals transferred from Milford to California, and Milford to Oxford. Morphology of the infectious organisms was identical in all of these episodes and the histopathology always consisted of acute inflammatory infiltration and systemic involvement. All episodes were associated with movement of oyster stocks originating in Milford, and all experienced severe mortality. No differences were noted between any of the *O. edulis* epizootics in regard to morphology of the organisms. Comparison of the American *O. edulis* infections with tissues of French oysters experiencing *B. ostreae* infections (Pichot et al. 1979; Balouet et al. 1983) revealed no morphologic or histologic differences at the light or electron microscope level. Indeed, ultrastructural comparisons demonstrate close similarities. Size comparisons of organisms are identical and the nucleus contains a peripheral nucleolus, and identical haplosporosome-like organelles are present in the cytoplasm. The major difference is in epizootic occurrences. The French epizootic occurred in natural or feral populations of European flat oysters. Since introduction of oysters to French sites from locations outside of France was a common event in the past, the source of the index case may have originated from an introduction of oysters from Elkhorn Slough, CA in the late 1970s (Elston et al. 1986). Contagious spread (Tige et al. 1981) is well documented in many locations in France and also the Netherlands. With the exception of the established breeding populations of flat oysters in the central Maine coast region, no natural or feral populations of *O. edulis* exist in the United States. The State of Maine carefully controls imports into the state; the disease has not been established in this population. The discovery of microcell infections in *O. lurida* in Oregon suggests that this may be a naturally occurring disease in that species. Infection intensity and prevalences suggest that some animals may die from the disease. The disease appears to be enzootic in the Oregon location. The lack of ultrastructural studies prevents close comparison of the *O. lurida* disease with the *O. edulis* disease. However, the disease in *O. lurida* tended to infect VCT while *B. ostreae* is primarily a disease of hemocytes.

CONCLUSIONS

There is a complex of oyster diseases caused by a group of protistan parasites of several species. These small intracellular and extracellular organisms designated originally as microcells have been found in association with serious disease in two species of *Crassostrea* and two species of *Ostrea*. It appears that the disease in *C. gigas* and *S. commercialis*, while exhibiting some similarities in types of lesions, are probably caused by different species of microcell type parasites.

A new genus, *Mikrocytos* g. n., and two new species have been described for the organisms causing disease in oysters: *Mikrocytos mackini* sp. n. in *C. gigas* from British Columbia, Canada, and *Mikrocytos roughleyi* sp. n. in *S. commercialis* from Australia.

Disease that has struck *O. edulis* in France is identical to the microcell disease seen in *O. edulis* in three episodes in the United States. The organism causing the disease in *O. edulis* is *Bonamia ostreae* and is clearly different from the microcell organism found in *C. gigas* in British Columbia and Hawaii. Finally, additional ultrastructural studies are needed for more complete characterization of the organisms from *O. lurida* and *S. commercialis*.

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NOTES

CONJOINED TWIN ADULT SHRIMP (DECAPODA: PENAEIDAE)

A two-headed roughback shrimp, *Trachypenaeus similis* (Smith), caught at the entrance to Galveston Bay, TX 10 May 1987 by Harold Fraley, together with a color photograph of the specimen taken subsequent to capture, was sent to me for identification, morphological examination, and deposit in the crustacean collection of the National Museum of Natural History (USNM 234419), Smithsonian Institution.

The specimen (Fig. 1) is composed of two cephalothoraxes (heads) perfectly aligned with the median sagittal plane and conjoined posteriorly to an unpaired, normally segmented abdomen. The cephalothoraxes and abdomen were disarticulated when the preserved specimen reached me in October 1987, but were restored to normal position easily with aid of the photograph as a guide. The lower cephalothorax is that of an adult female, carapace length including rostrum 32 mm, short carapace length (orbital margin to posteromedian edge of carapace) 21 mm; respective measurements for the upper carapace are 34.4 mm and 21.7 mm. The abdomen is flexed and twisted to the left, and the fourth and fifth segments are damaged, hence its length cannot be measured accurately. Comparison of the specimen with spermatophore bearing females of the species in the USNM crustacean collection indicates that it is adult in size, about 85 mm total length.

Shrimps are sometimes caught and preserved while in the act of molting. In that event the carapace being molted tends to be loosened at the thoraco-abdominal juncture so that its posterior end can be flipped dorsally and away, freeing the husk-like old carapace from the underlying soft new carapace. A first impression that this specimen was caught and preserved while in the act of molting was not borne out by the structures observed.

The integument of each carapace is firm, as is that of the other exoskeletal parts. Both carapaces are similar in shape and structure, including the part of the lower carapace that is hidden by the upper one. It is noteworthy that the upper carapace is larger than the lower, just the opposite of what would be expected if the upper one represented an ecdysial discard. Eyes in both heads have normal dark corneal pigment, though the corneal surfaces are shriveled by preservation. Antennules, anten-

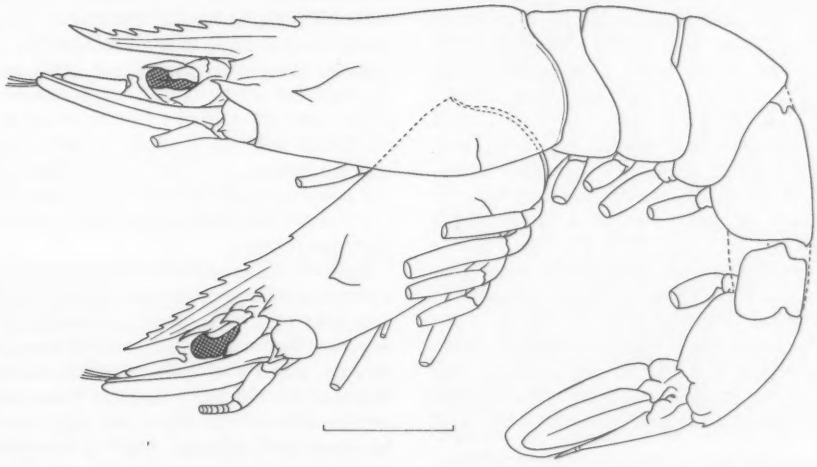

FIGURE 1.—Conjoined twin *Trachypenaeus similis* in diagrammatic lateral view, distal parts of appendages intentionally deleted, except for those of uropods. Scale = 1 cm.

nae, mandibles and associated palps, first and second maxillae, and first, second, and third maxillipeds are present and apparently normal on both heads, though the antennal flagella are broken and the right third maxilliped has apparently been lost from the upper head. Similarity in the cephalothoraxes is limited to features pointed out above.

The lower cephalothorax has normal appendages and internal organs, or traces of them, except for some broken and missing articles on the pereopods. The heart, hepatopancreas, and gonads apparently disintegrated during the interval of time between capture and fixation, hence lost all traces of their conformation in life. Fluids from the disrupted circulatory system were fixed as irregular clots. The mouth, esophagus, stomach, and a fragment of the gut are present, though the latter is connected neither to the pyloric stomach nor to the sector of intestine that courses through the abdomen to the anus. However, one can visualize that the path of the intestine in the lower cephalothorax was functionally normal before it was disrupted by breakdown of the other internal organs that surrounded it in life.

The upper cephalothorax lacks a mouth, the sternal plate between the mouthparts is not perforated, and there is no esophagus, stomach, or fragment of intestine. It seems therefore that the upper cephalothorax, though equipped with normal head appendages, could not function in feeding. Moreover, the rear part of the upper cephalothorax fitted over the rear part of the lower one like a firmly pulled down cap, with its branchiostegites deeply overlapping those of the lower one. In this arrangement the posterior part of the lower cephalothorax filled the space that would normally have been occupied by pereopods, external reproductive structures, thoracic endophragmal system and body wall, gills, and internal organs of the upper cephalothorax. As a result there was little or no room for development of these structures in the upper cephalothorax, although there may have been a heart. The membrane that lined the branchiostegites and body wall of the upper cephalothorax seems to have extended backward from the region of the cervical groove to merge with its counterpart in the posterior region of the lower cephalothorax, and with the normal integumental lining of the abdomen in order to have maintained confluence in the blood sinuses.

The abdomen, though crushed at the level of the fourth and fifth segments, bears normal pleopods, uropods, and telson. The anterior end of the abdominal muscle mass is preserved in a shape that fits the posterior end of both cephalothoraxes, but the main connection extended into the functional lower one in which complete organ systems were located.

There is a large literature treating malformations of decapod crustaceans, primarily lobsters, freshwater crayfishes, and crabs, but there is little published information of this sort on shrimps (Bateson 1894; Johnson 1968; Johnson and Chapman 1969; Pauley 1974), aside from the subject of disease which is not at issue here (Couch 1978). The most exhaustive account is that of Bateson who, along with many others before and after, discussed duplication of parts, intersexes, and malformations that occur during molting, Pérez Farfante (1980), for example, noted anomalous intersexes in the Indo-West Pacific needle shrimp, *Penaeopsis rectacuta* (Bate). The majority of these accounts treat malformed limbs or their parts (for a well-illustrated example see Shuster et al. 1963). Fewer studies are concerned with teratology.

Monsters with fused double cephalothoraxes, though rare, have long been known among larvae of the lobsters *Homarus americanus* H. Milne Edwards and *H. gammarus* (Linnaeus) (Herrick 1896, 1911). Ryder (1886) noted four forms of conjoined twins in larval American lobsters: lateral fusion of cephalothoraxes that demonstrated absence of eyes, possession of a single median eye or paired eyes representing the right eye of the right larva and left eye of the left larva, while the abdomens of each type were separate and divergent at a wide angle, and cephalothoraxes of two embryos fused together along their dorsal surfaces, with full complement of eyes, appendages, and separate abdomens, but with internal organ systems fused. Ryder attributed all of these twinnings to fusion coincident with the process of gastrulation and gradual formation of the embryos. Herrick (1896, 1911) discussed and figured some of these cases also but thought that fusion came later in development than gastrulation.

I have found no account of conjoined twinning in shrimps, and no report of twinning that parallels the case presented here. What is amazing is that an animal so bizarre could molt at all, let alone progress through a series of molts to attain mature size. Whether the deformity resulted from embryonic malformation or from subsequent injury cannot now be determined, although angle of divergence and median sagittal alignment of the cephalothoraxes suggests that the malformation resulted from aberrant molting.

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AUSTIN B. WILLIAMS

Systematics Laboratory
National Marine Fisheries Service, NOAA
National Museum of Natural History
Smithsonian Institution
Washington, DC 20560

NOTE ON MUSCLE GLYCOGEN AS AN INDICATOR OF SPAWNING POTENTIAL IN THE SEA SCALLOP, *PLACOPECTEN MAGELLANICUS*

During the reproductive cycle of the Atlantic sea scallop, *Placopecten magellanicus*, glycogen levels rise and fall in the hemolymph (Thompson 1977) and in the adductor muscle (Robinson et al. 1981; Gould 1983), reflecting the buildup of glycogen reserves in the muscle and their later transfer to the gonad. Muscle glycogen normally rises to a yearly peak in spring after the phytoplankton blooms, then is transferred to the gonad for gamete differentiation and maturation (Robinson et al. 1981). The glycogen transfer is followed by an increase in size of the maturing gonad and a loss of muscle weight (Gould 1983). During the autumnal algal blooms, glycogen levels in the muscle rise again slightly and drop thereafter to an annual low during the winter months, when the small energy reserves are used for basal maintenance and to initiate gametogenesis.

Glycogen reserves from the muscle and lipid reserves from the digestive gland are the major sources of stored energy supplied to the scallop gonad. High spring glycogen levels most dramatically indicate the degree of buildup of energy stores used to fuel gamete differentiation and maturation, whereas low winter muscle glycogen levels correspond to the postspawning exhaustion of reserves. Winter values higher than the normal range for any given population, therefore, could indicate an unusually large and extended period of nutrient availability, but more probably would suggest resorption of gametes.

We suggest, therefore, that the spring peak and the winter ebb of muscle glycogen be used as measures of the relative spawning potential and spawning success, respectively, for *Placopecten*. Sampling during these two seasons may readily provide information on the recruitment contribution of different scallop populations.

Timing of the seasonal high and low values for this metabolic parameter can vary by several weeks from year to year, reflecting the timing and intensity of phytoplankton blooms (themselves dependent on other environmental variables), and the time and degree of success in spawning. To obtain a practical data base for this major measure of seasonal energy reserves, therefore, we sampled a single bed of sea scallops off Asbury Park, NJ, on a year-round monthly basis for 3½ years. In examining mean annual high and low muscle glycogen values for these scallops, data were averaged for animal collections

from mid-April through June each year to arrive at a general value for the spring buildup and peak. Although such values do not indicate the maximal glycogen values, which may be reached either gradually or quickly in any of those months, an average better enables year-to-year comparisons. Data for collections from late November through February were similarly averaged to obtain a value for the postspawning winter period of low muscle glycogen.

We used this same parameter for specimens collected from random sites in the Gulf of Maine, and found a different seasonal pattern in scallops from depths greater than ca. 110 m. Because these deepwater sea scallops came from many different sites in the Gulf of Maine, data were averaged for each collection date for each site. This report presents our data for spring and winter adductor muscle glycogen in a single subtital sea scallop population for the years 1981–84, and in deepwater sea scallops from the Gulf of Maine for 1980–82.

Materials and Methods

Asbury Park sea scallops were collected by trawl from a site 31 m deep on the southern shelf of the Hudson River Canyon off Asbury Park, approximately 37 km NNE of Manasquan Inlet (ca. 40°13′ × 73°47′). Collections were made at monthly intervals from spring 1981 through late July 1984 and during two intensive weekly sampling periods from early May through mid-June in 1983 and 1984, to monitor the spring buildup of muscle glycogen. For some months, particularly in the spring of 1982, collections were not available. Each collection comprised 6 males and 6 females (shell height 95–110 mm). The sea scallops were held overnight in 5°C aerated seawater at the Northeast Fisheries Center's (NEFC) laboratory at Sandy Hook, NJ, and transported the following day in a cooler to the Milford, CT, NEFC laboratory. For transport, the sea scallops were placed on top of paper toweling that had been soaked in seawater, then wrung out and layered over ice enclosed in a sealed plastic bag. The animals were dissected the same day, and all tissue specimens were stored at −80°C until testing. Gonad volumes were also noted. Deepwater sea scallops were dissected on shipboard immediately after collection by trawl, and the muscle tissue held at −40°C while at sea, then transferred on dry ice to the −80°C freezer in Milford. Because we relied on volunteer help for many of these collections, gonad data were not always available for shipboard samples of adductor muscle from deepwater sea scallops.

Muscle dissection, tissue preparation, and the procedure for glycogen analysis are described in detail elsewhere (Gould et al. 1985); glycogen levels are presented as μg of glucose per gram of wet tissue (μg g^{-1}). Because there were no detectable differences between sexes for muscle glycogen levels, data for males and females were combined.

Results and Discussion

Asbury Park Sea Scallops

In the spring of 1981, the Asbury Park sea scallops had muscle glycogen levels averaging higher than 2,000 μg g^{-1} (Table 1). Such levels are not uncommon in well-fed scallop populations, as observed during several years of monitoring activity on the continental shelf off New England and the mid-Atlantic states (Gould 1981, 1983) during the NEFC's Ocean Pulse/Northeast Monitoring Program (NEMP) and the NEFC's Resource Assessment surveys. The mean annual low levels in the

TABLE 1.—Seasonal high and low levels in adductor muscle glycogen for both males and females in a single population of sea scallops off Asbury Park, NJ. Values were averaged for mean seasonal highs during and after spring phytoplankton blooms (April, May, June) and for mean seasonal lows after spawning (December, January, February). Gonad volumes are also shown for the same time periods.

Year	Season	Sample N	Muscle glycogen (μg g^{-1}) $\bar{x}$	Muscle glycogen (μg g^{-1}) SE	Annual ratio spring:winter	Gonad volume (mL) $\bar{x}$	Gonad volume (mL) SE
1981	Spring	34	2,217	283		no data	
1982	Spring	24	544	32		5.42	0.74
1983	Spring	84	610	15		6.23	0.29
1984	Spring	72	254	12		4.51	0.24
1981–82	Winter	22	203	18	10.9	6.50	0.47
1982–83	Winter	24	226	14	2.4	3.00	0.46
1983–84	Winter	12	490	57	1.2	2.75	0.39

Asbury Park sea scallops the following winter were within the normal range (200–300 $\mu g\ g^{-1}$) observed for sea scallop populations over those same years of monitoring.

In 1982 and 1983, the Asbury Park sea scallops were apparently adequately fed during the spring months, although glycogen levels were less than one third of those seen in 1981 and had no discernible peak. Muscle glycogen in the winter months of 1983 and 1984, however, was sufficiently high in both sexes (as compared with postspawning levels for this population, and with mean winter levels in other populations) to prompt the suspicion that gamete resorption had taken place, and that the 1983 spawning season had not been very successful. Moreover, although an intensive weekly sampling was performed in May and June 1984, we did not observe the normal seasonal increase in muscle glycogen; instead, the values resembled those of a typical winter low. When spring values for each year are compared with the subsequent winter's postspawning values (Table 1), a picture emerges of declining nutritional status from 1981 to the end of the study.

It is possible, of course, that the spring values in 1982 and 1983 were more typical for this population and that spring values for 1981 may have been unusually high. The latter phenomenon could have been the result of especially heavy phytoplankton blooms, or of oceanic currents favorable to the bottom settlement of planktonic nutrients. Certainly the most important single variable is nutrient availability.

The 1984 glycogen levels indicated either that little or no food was available to the sea scallops (at 30 m), or that they were not assimilating normally any food that was available. This phenomenon has yet to be explained satisfactorily, because the phytoplankton bloom in the area that year was extensive (J. O'Reilly[1]). Steven K. Cook[2] had suggested that some oceanographic event, such as the inshore intrusion of an offshore water mass known as the "cold pool" (e.g. Hopkins and Garfield 1979) may have caused an unusually early formation of a thermocline, one that effectively prevented settlement of planktonic detritus to the bottom. Whatever the reason, the Asbury Park sea scallops showed diminishing glycogen reserves for spawning from 1981 to the end of the study in 1984. Either planktonic nutrients were not reaching that population, or food was available but the sea scallops were not feeding or assimilating properly.

If the latter should be the case, it is perhaps relevant that the Asbury Park sea scallop population lies approximately 24 km downstream from the Christiaensen Basin, where general current patterns are southwesterly. Several active dumpsites are located in the Christiaensen Basin, including those for New York's sewage sludge and dredge spoils, where copper is a major contaminant (see Steimle et al. 1982). Moreover, as little as 10 $\mu g\ L^{-1}$ copper in the water column has been shown to interfere with gamete production and maturation (resorbing gametes) and probably also with feeding or nutrient assimilation in *Placopecten magellanicus* (Gould et al. 1985, 1988). Chemical analysis of tissues from these same Asbury Park sea scallops is under way, to determine whether metal levels were sufficiently elevated to induce this effect.

Deepwater Scallops

A data pattern for muscle glycogen similar to that seen in the Asbury Park sea scallops for 1984 has been observed in deepwater sea scallops taken from various sites in the Gulf of Maine (Table 2). These sea scallop beds were sampled randomly during the NEFC trawl survey cruises, and one fixed station was sampled seasonally during NEFC NEMP cruises (Gould 1981, 1983). Sea scallops taken from waters >110 m deep routinely showed very low glycogen levels throughout the year, the highest annual levels being reached in December. In the fall, vertical mixing of the subsurface and intermediate water increases to as deep as 150 m (McLellan et al. 1953; Colton 1968; Hopkins and Garfield 1979; Mountain and Jessen 1987), with the disappearance of any strong thermocline. In a recent comparison of food resources in shallow (20 m) and in deepwater (180 m) populations, Shumway et al. (1987) observed that a number of intact planktonic algal species reached the deepwater sea scallops after the fall phytoplankton bloom; this late annual food source "may provide just enough energy to sustain the population." On the whole, however, nutrient availability is very low at such depths, as indicated by the absence of chlorophyll in the deeper water column (J. O'Reilly[3]).

Deepwater sea scallops are visibly undernourished

[1]J. O'Reilly, Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 428, Highlands, NJ 07732, pers. commun. October 1984.

[2]Steven K. Cook, National Weather Service, 2980 Pacific Highway, San Diego, CA 92101, pers. commun. March 1984.

[3]J. O'Reilly, Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 428, Highland, NJ 07732, pers. commun. May 1985.

TABLE 2.—Mean seasonal high and low levels of adductor muscle glycogen in deepwater sea scallop populations of the Gulf of Maine.

Station coordinates		Date of collection	Depth (m)	Bottom temperature (°C)	Sample *N*	Mean gonad volume (mL)	Muscle glycogen ($\mu g\ g^{-1}$)
Lat.	Long.						
43°21′	[1]69°03′	01/29/82	160	7.0	12	2.25	153
43°23′	69°55′	04/23/80	168	4.2	5	—	303
43°25′	69°22′	04/23	180	4.9	5	—	164
43°16′	69°40′	04/23	159	4.0	5	—	248
43°20′	69°03′	05/07	155	5.0	5	—	282
43°21′	67°06′	05/07	155	5.0	4	—	274
42°49′	68°49′	05/10/81	202	6.0	2	—	145
43°07′	68°42′	05/10	174	5.5	8	—	199
43°30′	69°30′	05/24	144	4.2	12	—	178
43°33′	69°07′	05/24	152	8.4	4	—	180
44°21′	67°21′	08/03/82	137	10.4	12	4.70	178
42°56′	70°16′	08/16/80	155	4.9	8	—	226
43°26′	69°57′	08/16	134	5.3	9	—	120
43°21′	[1]69°03′	08/24/82	156	5.5 (at 100 m)	12	8.67	361
43°21′	[1]69°03′	09/07/80	155	6.0	18	9.09	133
43°17′	69°18′	11/04/80	161	6.0	10	—	437
43°18′	69°03′	11/04	167	7.2	10	—	330
43°00′	69°20′	11/04	181	5.8	10	—	318
43°37′	69°32′	11/04	113	8.1	5	—	582
43°21′	[1]69°03′	12/06/82	160	7.5	12	2.42	587
43°25′	69°22′	12/06	162	10.0	12	3.75	495
43°18′	70°03′	12/07	158	7.2	12	2.67	409
42°59′	70°10′	12/07	183	7.8	13	2.58	424

[1]Deepwater station off Toothaker Ridge that was sampled whenever possible; other stations were selected randomly during resource survey cruises.

(thin shells and small adductor muscles), lack the necessary glycogen reserves for successful spawning, and very probably resorb gametes. Moreover, bottom temperatures seldom reach 10°C (Mountain and Jessen 1987), the lowest temperature at which *Placopecten magellanicus* has been observed to spawn (Culliney 1974). In a recent study of a single deepwater sea scallop population in the Gulf of Maine, Barber et al. (1988) report reduced fecundity, followed by gamete resorption and a possible minor spring spawning, in turn followed by redevelopment, continued resorption, and an abrupt fall spawning attempt. Almost certainly, deepwater sea scallops do not spawn successfully. Recruitment to these beds, therefore, would be haphazard and originate both from populations on nearby ledges and from spatfall out of the Gulf of Maine gyre, from upstream spawning populations.

We have reported here that glycogen levels in *Placopecten magellanicus* adductor muscle, measured during the annual peak period in late spring and during the annual low period in winter, can indicate scallop populations with little energy reserves for successful spawning. In the case of the deepwater sea scallops in the Gulf of Maine, lack of available nutrients is undoubtedly the reason for their low muscle glycogen. Still to be clarified are the events leading to the 1984 failure of the Asbury Park sea scallops to develop the necessary energy reserves for spawning.

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EDITH GOULD
DIANE RUSANOWSKY
DONNA A. LUEDKE

Northeast Fisheries Center Milford Laboratory
National Marine Fisheries Service, NOAA
212 Rogers Avenue
Milford, CT 06460

VERTICAL DISTRIBUTION AND MASS MORTALITY OF PRAWNS, *PANDALUS PLATYCEROS*, IN SAANICH INLET, BRITISH COLUMBIA

Prawn, or spot prawn, *Pandalus platyceros* Brandt, 1851, British Columbia's largest shrimp species, is extensively fished in Canada and is of considerable economic importance (Noakes and Jamieson 1986). The species ranges from California to Alaska and, being largely associated with rocky terrain, is fished with traps in many of the region's coastal inlets (Butler 1980).

This study reports a fortuitous observation of catastrophic mortality of prawn in Saanich Inlet, noted during a series of observations on the vertical distribution of prawn on the walls of this fjord using a submersible. These observations are important because, under the circumstances involved, these mobile benthic organisms had ample opportunity to avoid the apparent rapid intrusion of lethal environmental conditions by moving upwards, and thereby remaining in a favorable environment.

Well-documented sudden mass deaths of adult marine invertebrates in subtidal environments have usually been associated with man-induced environmental perturbation, such as an oil spill, pollutant discharge, entrainment of organisms into a lethal environment (e.g., dredge or power plant cooling water intake), or the entrapment of benthic organisms by some lethal environmental event (Tulkki 1965). However, the selective high mortality of one or only a few species in a subtidal community, with no associated physical habitat perturbation and with apparent opportunity for escape, has been infrequently described in documented catastrophic mortalities (Brongersma-Sanders 1957; Swanson and Sindermann 1979; Levings 1980a, b; Tunnicliffe 1981; Burd and Brinkhurst 1984, 1985; Renaud 1986). It is known that species differ in their relative tolerances to environmental stress (e.g., Renaud 1986), but for subtidal invertebrates, the proximity to lethal conditions of the majority of a population for extended time periods has not been generally noted. This study shows that prawn may occur close to lethal environmental conditions, and that abrupt mortality results if lethal water conditions suddenly intrude. In certain locations, such mortality may be more frequent than previously recognized and may justify a unique exploitation strategy.

Materials and Methods

This study was conducted between 6 and 10

October 1986, at Bamberton (lat. 48°35′N, long. 123°31′W), located half-way down Saanich Inlet, a 24 km long fjord on the southeast coast of Vancouver Island. Because of its close proximity to regional oceanographic laboratories, this inlet has been well studied oceanographically (Carter 1934; Herlinveaux 1962; Richards 1965; Anderson and Devol 1973; Pickard 1975; Emerson et al. 1979; Thomson 1981) and biologically (Tunnicliffe 1981; Burd and Brinkhurst 1984, 1985). At its mouth, it has a submerged (75 m) sill behind which there is a deep (maximum depth = 234 m) basin, and water below the sill depth is typically isolated, oxygen-deficient, and may contain hydrogen sulphide. The basin is flushed only when water above the sill is sufficiently dense to cascade into it. Throughout the year, there typically remains one or more oxyclines in the water column structure. The study area is generally characterized by a 20–30° slope to about 70 m, and a 30–60° slope from this depth to the bottom of the inlet (209 m).

Observations were made by two people from the submersible *Pisces IV*, which has been previously described by Mackie and Mills (1983). Two 3-h dives were made each day—one typically starting at 1300 and the other at 1900, about one hour after sunset. Dives to the bottom of the inlet were conducted at random locations over a 3 km length of shoreline and began with a direct descent to the bottom of the inlet. The submersible was then moved upwards, horizontal and about 1 m from the cliff, from the bottom of the inlet to a depth of 20 m. After surfacing, the submersible was then towed to another dive location, where the process was repeated. A total of 17 ascents were completed during the 8 dives.

Ascent speed varied according to habitat complexity, slope, and crustacean abundance, but was slow enough to permit recording of the species observed except in areas where extremely dense concentrations of animals were found. Observers were stationed on opposite sides of the submersible, with no overlap in their visual field. Each observer was able to scan approximately 90° on one side of the submersible's path.

As discussed by Richards and Schnute (1986), a general problem with use of submersibles has been the quantification of species abundance. Both the presence of lights and the submersible itself might affect animal behavior and hence bias observations. Prawns tend to be cryptic and were frequently found in association with bottom debris, and occasionally in holes. After extensive observations, including moving at specific locales with lights on or off and moving at variable speeds, it was concluded that prawns and other demersal crustaceans were not apparently affected by *Pisces*'s presence, allowing them to be effectively studied. On the approach of *Pisces*, demersal crustaceans would occasionally swim a short distance with rapid flicks of their abdomens, but in most cases, they would simply assume an aggressive stance towards the submersible and continuously face it as it passed by. They did not retreat under cover.

Visibility of benthic animals varied somewhat because of changes in bottom topography and its effect on distance of the submersible from the substrate. Water clarity was generally good (>7 m), but resolution was poor at the perimeter of the illuminated area (about 5 m maximum).

Data were initially recorded into handheld tape recorders, and tapes were transcribed shortly after each dive. Prawns were individually counted and their depths of occurrence noted over a vertical transect of about 3 m. However, this procedure could not be used when live prawn abundance exceeded approximately 6 m^{-2}, because of their high density and because the prawns stirred up the substrate by their movements. This situation only occurred over a narrow depth range (between 70 and 85 m depth, depending on date of observation). Dead prawns, which often only consisted of exoskeleton fragments, were also difficult to count at a density greater than about 2 m^{-2}. In both situations, number per meter of depth was conservatively estimated by multiplying the respective minimum average density per square meter by 3 m, the transect width over which live and dead prawn abundances were being assessed.

Qualitative notes on abundance of munids, *Munida quadraspina* Benedict, 1902, the dominant benthic crustacean present, were recorded by depth interval. Observers noted other invertebrate and fish species present in each transect.

Movement of observed crustaceans was sufficiently slow, relative to the submersible's movement, to prevent their crossing the submersible's path and possible double counting by the observers. Body size of some individuals was estimated by comparing them to a 30 cm rod, marked in 10 cm intervals, that hung in front of the left viewport. Sizes were later confirmed by measurement of carapace lengths of specimens collected using the extendable arm of the submersible.

Water samples, and on some occasions crustaceans, were collected at selected depths by pumping water through jars attached to the exterior of the submersible until they had been thoroughly

flushed, and then sealing them. Samples were fixed with manganous sulphate reagent and alkaline iodide solution as soon as the submersible had surfaced and was recovered at the end of each dive, and dissolved oxygen concentrations were determined later using a modified Winkler titration procedure (Strickland and Parsons 1972). Ambient water temperature was recorded continuously during each dive. On 14 October 1986, a more comprehensive set of oceanographic measurements (temperature, salinity, and dissolved oxygen [DO_2]) was obtained by University of British Columbia (UBC) oceanographers 1 km from the study area.

Results

Substrate type was a soft, light-brown flocculent ooze at the bottom of the inlet up to a depth of about 60 m, when it became more gravelly. The floor of the inlet was relatively flat, changing to a slope of 30–60° at the walls up to a depth of about 100 m, at which point 5–10 m vertical rock cliffs often occurred. The slope then lessened at approximately 70 m depth to 20–30°, with frequent rock outcroppings observed up to the minimum depth (20 m) surveyed.

Salinity and temperature below 20 m ranged from 30.0 to 31.4‰ and from 8.0° to 11.2°C, respectively, throughout the study. During the first two days of observations, measured DO_2 levels were >1 mL · L^{-1} at depths above 20 m. Between the afternoon and evening dives of the third day (8 October), an abrupt decrease in DO_2 concentration to between 0.76 and 0.92 mL · L^{-1} was detected at depths of 75–77 m. However, at nearby depths of 71–73 m, DO_2 levels remained above 1 mL · L^{-1} (1.29–2.00 mL · L^{-1}).

Dissolved oxygen (DO_2) measurements obtained during the last two days of our study show a similar profile to those obtained four days later in the center of the inlet by the UBC team (Fig. 1). In both cases, a region of low DO_2 (<1 mL · L^{-1}) was seen in waters of intermediate depth, although the depth at which this lens of low DO_2 occurred differed by about 20 m. Minimum DO_2 level recorded during our dives was 0.76 mL · L^{-1} at 77 m on 8 October, while on 14 October in the center of the inlet, the lowest value noted was 0.44 mL · L^{-1} at 110 m. Since low DO_2 levels normally occur in the deepest waters of the inlet (Pickard 1975; Burd and Brinkhurst 1984), these results indicated that there had recently been intrusions of denser, more oxygenated water over the sill into the deeper regions of the inlet, displacing the low DO_2 layer upwards or advecting low DO_2 water into the study area.

There were clear differences in depth ranges inhabited by species commonly observed in the study area (Fig. 1). The species we observed were primarily benthic in habit, although some epibenthic species such as spotted ratfish, *Hydrolagus colliei* (Lay and Bennet, 1839); spiny dogfish, *Squalus acanthias* Linnaeus, 1758; and Pacific cod, *Gadus macrocephalus* Tilesius, 1810, were periodically observed, usually at depths below 80 m. Various rockfish (*Sebastes* sp.) were observed around rock outcroppings.

The most abundant benthic invertebrate species observed below 60 m were four species of shrimp (*Spirontocaris holmesi* Holthuis, 1947; *S. sica* Rathbun, 1902; pink shrimp, *Pandalus jordani* Rathbun, 1902; and prawn) and munids. A few Dungeness crab, *Cancer magister* (Dana, 1851) were observed at 40–80 m depth. Greatest densities of prawns generally occurred between 70 and 85 m depth, although their observed range was from 20 to 159 m (Table 1). There was no obvious difference in the depth range of major prawn concentration (70–85 m) between afternoon and night dives on the same day. However, more prawns were observed in the depth range of 20–70 m at night than during the day, but these were relatively few in comparison to those at 70–85 m depth (Table 1). During the latter part of the study, most prawns were in a narrow band between 70 and 79 m depth. An amphipod, *Orchomene obtusa* (Sars, 1890), was common on the substrate from 80–210 m water depth. Major concentrations of pelagic amphipods were observed at depths of 45–75 m and 23–90 m during the day and night, respectively. Euphausiids were most abundant at 90–135 m during the day and at 50–90 m at night.

Munids were not observed above the main prawn concentration at 70–85 m. A wide size range of munids was observed, ranging from recently settled juveniles to adults of about 3 cm carapace length. In general, large individuals were found below 100 m whereas small munids were found from 80 to 120 m depth. Munids were observed down to the deepest depth surveyed (209 m).

On the evening dive of the third day, 8 October, dying and dead prawns, the latter covered with swarms of amphipods, were observed between 82 and 90 m depth, with most between 85 and 90 m (Table 1). Some live prawns showing disoriented behavior were also observed. Examination of collected live prawns observed to be in poor condition when sampled showed no evidence of disease or

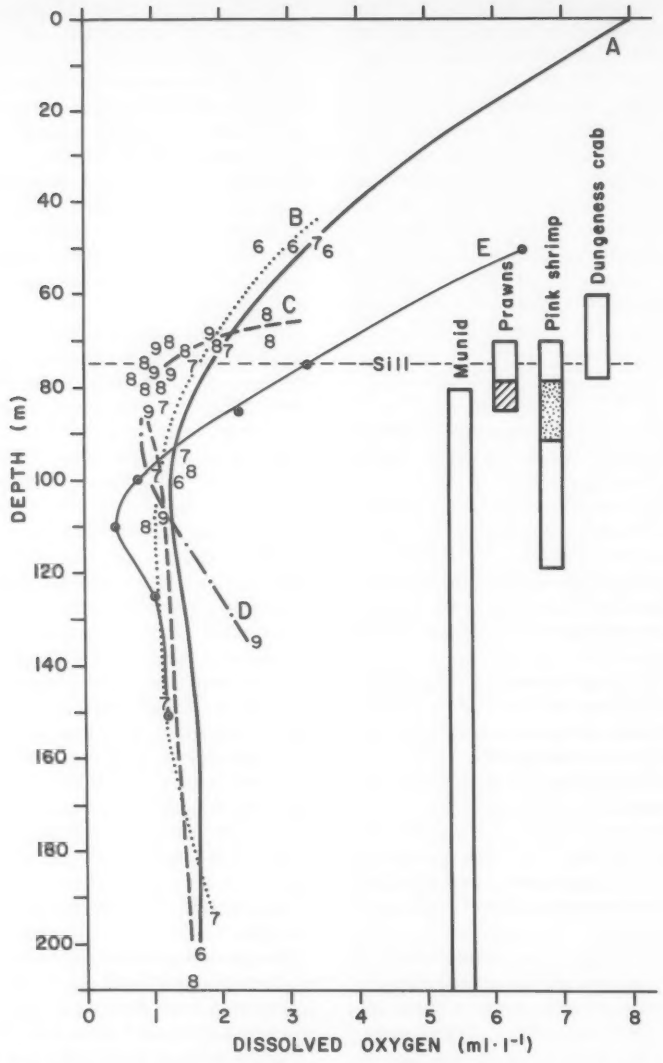

FIGURE 1.—Dissolved oxygen levels (mL · L^{-1}) at depth during each of the 4 days of diving (lines were drawn by eye) and for the UBC sampling, and relative depth distributions of the main abundances of the four large crustaceans observed. Oblique bar = zone of prawn mortality; stipple = area devoid of pink shrimp after low DO_2 water intrusion. Numbers = dates in October 1986. A (——) = 6 October, B (•••) = 7 October, C (– – –) = 8 October, D (–•–•) = 9 October, E (•—•) = 14 October (UBC profile).

TABLE 1.—Average prawn abundance per observer per 5 m depth increment observed in the depth range 20–124 m during the 4 days of observations, 6–9 October 1986. A = afternoon dive, E = evening dive, numbers in brackets = no. of ascents, no. of observers, < > = dead or dying.

	6 October		7 October		8 October		9 October	
Depth (m)	A (2,1)	E (2,2)	A (1,1)	E (2,1)	A (1,1)	E (3,2)	A (3,2)	E[1] (3,2)
20–24	0	0	0	1.5	0	0	0	—
25–29	0	0	0	1.5	0	0.5	0	—
30–34	0	0	0	3.5	0	0	0	—
35–39	0	0.25	0	4.5	0	0.5	0	—
40–44	0	1.00	0	2.5	0	2.0	0	—
45–49	0	2.0	0	2.0	0	0	0	—
50–54	0	2.5	0	0	0	0	0	—
55–59	0	7.0	0	0.5	0	0	0	—
60–64	0	10.0	1.0	1.0	0	0.5	0	—
65–69	0	14.25	0	5.0	0	1.0	0.6	3.0
70–74	1.0	[2]54.0	38.0	9.0	[2]80.0	2.0	[2]36.0	[2]80.0
75–79	[2]80.0	[2]80.0	0	[2]80.0	0	[2]80.0	[2]80.0 < 8>	[2]80.0
80–84	[2]80.0	[2]36.0	0	0	0	[2]16.0 <[3]18>	0 <[3]12>	[2]36.0 <[3]18>
85–89	0.5	1.0	0	0	0	0 <[3]30>	0 <[3]30>	0 <[3]30>
90–94	0.5	1.5	0	0	0	0 < [3]6>	0 <0.3>	0 <[3]12>
95–99	2.5	0.75	0	0	0	0	0	0 < 4>
100–104	2.0	0.75	0	0	0	0.3	0	0
105–109	2.5	2.75	0	0	0	0	0.25	0
110–114	3.0	4.25	0	0	0	0	0	0
115–119	2.0	0.25	1.0	0	0	1.0	0.25	0
120–124	0.3	1.5	0	0	0	0	0.25	0
Total alive	174.3	219.0	40.0	111.0	80.0	103.8	117.4	199.0
Total dead	0	0	0	0	0	54.0	50.3	64.0
Estimated mortality (%)	0	0	0	0	0	34	30	24

[1]No observations were made above 65 m on the evening of 9 October because of the entanglement of *Pisces* in submerged rope. Recorder equipment failure prevented inclusion of one of the observer's counts of prawn on some of the dives.

[2]Live prawn abundance was estimated >6 m^{-2}, but for purposes of analyses, 6 m^{-2} × 3 m^2 visibility was assumed, giving 18 prawn per meter of water depth.

[3]Dead prawn abundance was estimated >2 m^{-2}, but for purposes of analyses, 2 m^{-2} × 3 m^2 visibility was assumed, giving 6 dead prawn per meter of water depth.

parasitism (S. Bower[1]). Dead prawns, sometimes consisting only of exoskeleton remains, were observed at a density >2 m^{-2} in some areas. Apparently healthy prawns were concentrated in the depth range of 75–80 m at densities >6 m^{-2}. Dead and dying prawns were also observed during both dives on 9 October. By comparing the estimated numbers of dead and living prawns observed in a vertical transect, it was conservatively estimated that approximately 25% of the prawn population observed may have died during this 24-h period, with observations taken over 9 ascents along about 1.5 km of shoreline (Table 1).

Prawn was the only species observed to be dying. Apparently healthy amphipods, munids, and flatfish were observed around the dying prawns. However, coincident with the onset of prawn mortality, the vertical distribution of pink shrimp separated into two groups, one above and one below the depth range of prawn mortality (Fig. 1). No dead pink shrimp were observed. Only amphipods were observed eating the dying or dead prawns.

Discussion

Our observations indicate that the tolerance of prawn to low DO_2 levels may be less than that reported from laboratory experiments. The tolerance of prawn in a sealed chamber (10°C, 30‰ salinity) to low DO_2 levels has been experimentally examined by Whyte and Carswell (1982). Under their experimental conditions, prawns exhibited a reduced metabolic rate at DO_2 levels below approximately 2.5 mL · L^{-1} and died at approximately 0.35 mL · L^{-1}. They did not determine how long prawns would survive at dissolved oxygen levels below 1 mL · L^{-1} since their experimental design included only a fixed amount of oxygen. Our study suggests that minimum tolerance occurs at around 1 mL · L^{-1} since at levels below this, death occurred. Oxygen stress in munids has been reported (Burd 1983) to coincide with a loss of equilibrium similar to the disoriented locomotor behavior we observed for

[1]S. Bower, Pacific Biological Station, Nanaimo, B.C., V9R 5K6, pers. commun. October 1986.

prawns. Based on our observations, we further note that prawns appear to be less tolerant to low DO_2 levels than many of the other species found in the same depth range. However, published data on tolerance to hypoxic conditions for the species present exists only for munids, which have been shown to tolerate hypoxic conditions as low as 0.1–0.15 mL · L^{-1} (Burd 1983; Burd and Brinkhurst 1984, 1985).

All benthic species observed, except prawn, had a relatively large depth range over which individuals were found in abundance. Those species apparently more tolerant to low DO_2 levels were found from about 85–210 m. It is unknown why in contrast to other species observed, prawns were concentrated in a narrow depth range at 70–85 m water depth, so close to lethal water conditions. Most prawns were apparently prevented from going deeper by intolerance to low DO_2 concentrations, although a few individuals were below this low DO_2 layer and, for the short term at least, were apparently surviving. At night, there was little change in the observed general depth preference of the main prawn concentration, although more prawns were observed at shallower depths. Prawns were not observed moving vertically on the cliffs in a directed manner, and so prawns observed at shallower depths at night may have been hidden there during the day.

With the sudden movement of low DO_2 water into the depth range occupied by prawns, it is unknown why prawns did not simply walk upwards on the cliff, away from the low DO_2 area, and stay in a tolerable environment, as did the pink shrimp. The distance prawns would have had to travel was <10 m in the 70–75 m depth range. Some vertical movement of prawns may have occurred, since in the afternoon dive prior to the evening dive in which dead prawns were first observed, the depth range in which prawns were abundant was narrow (5 m) and at its shallowest depth (70–75 m).

Two oceanographic factors apparently caused the observed prawn mortality: the existence of a low DO_2 water mass in close proximity to the prawns and some event which caused this water mass to intrude suddenly into the prawn habitat. As indicated earlier, the presence of oxyclines in Saanich Inlet is well documented, although the close proximity of prawns to this lethal environment had not previously been described.

We offer two possible explanations that could account for sudden intrusion of the anoxic layer: 1) change in the amplitude of oscillations of the oxycline, or 2) an overall change in level of the mean oxygen surfaces, perhaps related to a change in subsurface properties. With respect to the first, Thomson et al. (in press) showed that in Saanich Inlet, there are regular, peak-to-peak oscillations in DO_2 level of the order of 2.5 mL · L^{-1} at 100 m depth. These oscillations were found to occur over a period of hours, with a standard deviation and range of effective vertical isopycnal displacement estimated to be 2.0 and 9.6 m, respectively. Thomson et al. (in press) collected their data in April 1987, when the mean DO_2 level at 100 m was 4.8 mL · L^{-1}. If similar oscillations of the oxycline occurred during our observations, when DO_2 levels were much lower, then with a moderate change in oscillation amplitude, prawn could suddenly experience lethal DO_2 levels for time periods up to approximately 6 hours. The causal mechanism generating the oscillations and changes in amplitude of oscillation of the pycnocline, and hence oxycline, is currently unknown, but is probably due to internal gravity waves propagating within the inlet (R. Thomson[2]).

The second explanation involves a rapid change in average depth of the oxycline caused by changes in vertical density profile of the water column. Intermediate depth waters outside Saanich Inlet are most dense in the fall, and intrusion of this denser water over the sill into the inlet typically occurs at this time (Pickard 1975). Such intrusions are often caused by strong tidal influxes, and fluctuations in depth of the pycnocline and oxycline subsequently propagate down the inlet as a density intrusion (Holbrook and Halpern 1982). Any intrusion has the potential of suddenly altering oxygen concentrations at various depths. The observation of mortality beginning in late afternoon on 8 October is in agreement with that expected based on the daily and hourly timing of tidal action seen during the study period.

Prawn mortality as described would thus appear to be an episodic, but perhaps not an uncommon, event in Saanich Inlet. It is probably a fall phenomenon, for the oceanographic reasons described above and since in other years, this was when the hypoxic layer was shallowest (Richards 1965; Tunnicliffe 1981; Burd and Brinkhurst 1984). Our observations clearly demonstrate that sudden catastrophic mortality can occur on a scale which may noticeably affect species abundance in an area. If undocumented, such episodic mass mortality may confound an understanding of species population dynamics. For fishermen in the area, mortality of prawn is a concern and may explain why seasonal landings may

[2]R. Thomson, Institute of Ocean Sciences, Sidney, B.C. V8L 4B2, pers. commun. May 1987.

not meet expectations. Understanding the timing and likelihood of such events can improve management, and since the geographical occurrence of such mortality may often be quite localized, increased harvest in specific locations prior to high natural mortality events might be justified.

Acknowledgments

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GLEN S. JAMIESON

Department of Fisheries and Oceans
Fisheries Research Branch
Pacific Biological Station
Nanaimo, British Columbia V9R 5K6, Canada

ELLEN K. PIKITCH

Department of Fisheries and Wildlife
Oregon State University
M. O. Hatfield Marine Science Center
Newport, OR 97365
Present address:
School of Fisheries WH-10
University of Washington
Seattle, WA 98195, USA

MORPHOLOGICAL DIFFERENCES BETWEEN TWO CONGENERIC SPECIES OF PLEURONECTID FLATFISHES: ARROWTOOTH FLOUNDER, *ATHERESTHES STOMIAS*, AND KAMCHATKA FLOUNDER, *A. EVERMANNI*

The two flatfishes of the genus *Atheresthes* (family Pleuronectidae) are commonly caught in the eastern Bering Sea commercial trawl fishery. From 1977 to 1983, they comprised an estimated 10.03% of the total flatfish catch by the foreign trawl vessels in the Bering Sea/Aleutian Islands region (data compiled from U.S. Foreign Fisheries Observer Program, Northwest and Alaska Fisheries Center). However, these two species, the arrowtooth flounder, *A. stomias*, and Kamchatka flounder, *A. evermanni*, are morphologically similar and hence difficult to distinguish. As a result, fisheries workers in the field often lump the two species or misidentify them. Because the two species may have biological differences not presently known, it is important for management considerations and stock assessments to distinguish the species in fisheries surveys. The objective of this paper is to describe gross morphological differences between the two species more explicitly, so that the two can be accurately identified in the field.

Norman (1934) thought that these two species of *Atheresthes* were so similar that eventually they were shown to be identical. However, based on electrophoretic evidence, Ranck et al. (1986) concluded that *A. stomias* and *A. evermanni* are valid species. Wilimovsky et al. (1967) previously had reached this same conclusion by using a special morphological character index to separate the two species. This index is a function of caudal vertebrae number, gill raker number, distance from anterior eye margin to dorsal origin, and eye diameter. Unfortunately, the index is too complex to use in the field because it is based partly on characters that cannot easily be evaluated by gross external examination. This study describes a simpler method for differentiating the two species based on previously described external morphological characteristics and two new morphological characters.

Methods

Collections were made in the eastern Bering Sea in an area between lat. 54° and 59°N, long. 163° and 174°W (Fig. 1) aboard the National Marine Fisheries Service RV *Chapman* in summer 1984.

Specimens were unselectively sampled in the field from trawl catches containing *A. stomias* and *A. evermanni*. The fork length and sex of the fish along with location of sample were recorded, and each specimen was preserved in 3.7% seawater/formaldehyde solution.

In the laboratory, the following characteristics were examined:

1) Upper eye position: Specimens were first classified according to the position of the upper eye, following Norman (1934). If the orbit of the upper eye interrupted the profile of the head (Fig. 2A), the specimen was classified as *A. stomias*. If the upper eye did not interrupt the profile of the head (Fig. 2B) and was completely on the right side of the head, the specimen was classified as *A. evermanni* (Norman 1934; Wilimovsky 1967).

2) Gill raker counts: After initial separation of the specimens on the basis of the upper eye position, the four gill arches of the eyed side were removed and the gill raker count of each of the four arches recorded. Counts of the upper and lower limbs were recorded separately and the two counts were separated by a plus sign (for example, 4+12 means 4 rakers on the upper limb and 12 on the lower limb). If a gill raker straddled the angle of the arch, it was included in the count of the lower limb. In this study, only the lath-shaped structures were counted as gill rakers; the rudiments were not counted.

Results

A total of 251 fish was examined. Based on the upper eye position, 170 specimens were classi-

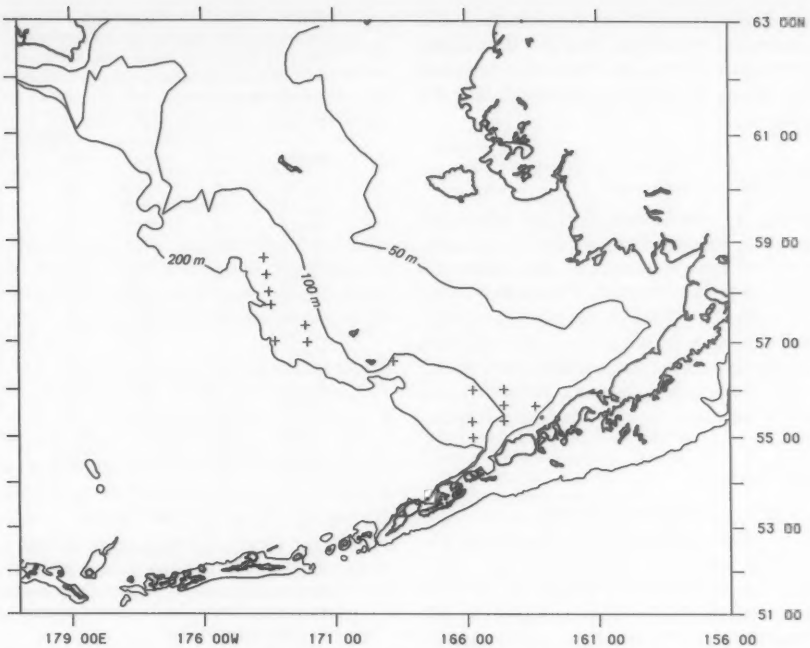

FIGURE 1.—Bering Sea collecting localities.

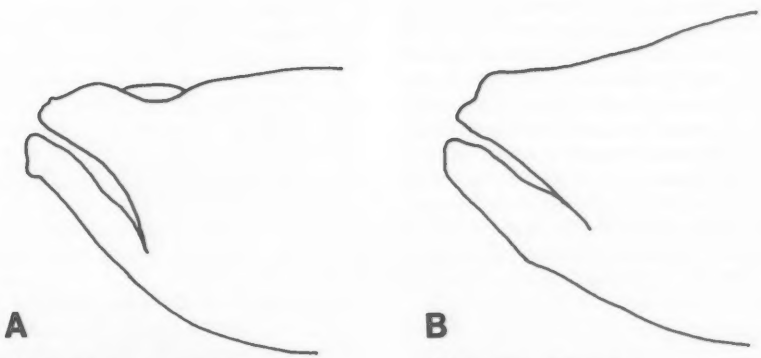

FIGURE 2.—Blind side view of head profiles of *Atheresthes stomias* (A) and *A. evermanni* (B).

fied as *A. stomias*, and 81 as *A. evermanni*. Gill rakers decreased in number from the first to the third gill arches in both species. Neither species had gill rakers on the fourth gill arch (though they did have rudiments).

First Gill Arch

In general, *A. stomias* had more gill rakers (on both the upper and lower limbs) on the first gill arch than did *A. evermanni*; however, the counts did overlap both in arrangement of gill rakers and total numbers (Table 1). Of the *A. stomias* examined, 75.2% had 4 or more rakers on the upper limb and none had fewer than 3. On the other hand, no *A. evermanni* had 4 or more gill rakers, and 49.4% had 2 rakers on the upper limb on the first gill arch.

Second Gill Arch

As was the case of the first gill arch, *A. stomias*, in general, had more gill rakers on the second gill arch than did *A. evermanni*. There were minor overlaps (1.8%) between these two species in the total gill raker counts and in the distribution of the gill rakers (Table 2). In addition to having different gill raker counts and patterns, all of the *A. evermanni* examined had 1 gill raker on the upper limb of the second gill arch, whereas 98.2% of the *A. stomias* had 2 gill rakers on the upper limb of the second gill arch (Table 2).

Third Gill Arch

In general, *A. stomias* had more gill rakers on the third gill arch than did *A. evermanni*. The range of total raker counts for *A. stomias* was 3 to 7, with most (85.3%) having 4 or 5. Total raker counts for *A. evermanni* ranged from 2 to 5, with 64.2% having 3. The most frequent arrangements of gill rakers on the third gill arch of *A. stomias* were 0+4 (43.5%) and 0+5 (41.2%), and the most frequent arrangement for *A. evermanni* was 0+3 (64.2%). Only three (1.8%) *A. stomias* had one gill raker on the upper limb of the third gill arch. The rest (98.2% *A. stomias* and all *A. evermanni*) had no gill rakers on the upper limb of the third gill arch.

Anomalous Specimens

Three specimens had the upper eye interrupting the profile of the head but had only 1 gill raker on the upper limb of the second gill arch. These fish were probably *A. stomias* with anomalous gill raker counts. One of the three had gill raker patterns of 4+11, 1+9, and 0+4 on the first, second, and third gill arches, respectively. The gill raker patterns on the blind side of this specimen were 3+11 on the first gill arch, 2+9 on the second, and 0+4 on the third. Thus, because this specimen had 4 gill rakers on the upper limb of the first gill arch on the eye

TABLE 1.—Gill-raker arrangements and their percentages (%) of frequency of occurrence (FO) on the first gill arches (eyed side) of *Atheresthes stomias* and *Atheresthes evermanni* collected from eastern Bering Sea.

	stomias		*evermanni*	
Pattern	FO	%	FO	%
5+11	2	1.2	0	0
4+13	1	0.6	0	0
4+12	59	34.7	0	0
4+11	65	38.1	0	0
4+10	1	0.6	0	0
3+13	1	0.6	0	0
3+12	11	6.5	0	0
3+11	29	17.1	4	4.9
3+10	1	0.6	32	39.5
3+9	0	0	5	6.2
2+11	0	0	3	3.7
2+10	0	0	29	35.8
2+9	0	0	8	9.9
Total	170	100	81	100
Mean	15.1		12.4	

TABLE 2.—Gill-raker arrangements and their percentages (%) of frequency of occurrence (FO) on the second gill arches (eyed side) of *Atheresthes stomias* and *Atheresthes evermanni* collected from the eastern Bering Sea.

	stomias		*evermanni*	
Pattern	FO	%	FO	%
3+10	1	0.6	0	0
2+11	3	1.8	0	0
2+10	54	31.8	0	0
2+9	108	63.4	0	0
2+8	1	0.6	0	0
1+9	3	1.8	8	9.9
1+8	0	0	61	75.3
1+7	0	0	11	13.6
1+6	0	0	1	1.2
Total	170	100	81	100
Mean	11.3		8.9	
2 or more rakers on upper limb	167	98.2	0	0
1 raker on upper limb	[1]3	1.8	81	100

[1]All of these *A. stomias* have two gill rakers on the upper limbs of the second gill arches of the blind side. Their patterns are either 2+10 or 2+9.

side and 2 gill rakers on the upper limb of the second gill arch on the blind side, it is referred to *A. stomias*. The other two anomalous specimens also had 2 gill rakers on the upper limbs of the second gill arch of the blind side and were also recorded as *A. stomias*.

Discussion

From this study, it is evident that the two species of *Atheresthes* can most easily be distinguished by eye position. The number of gill rakers on first and second gill arches can be used to assist and verify identification.

When identifying specimens, eye position should be examined first. If the upper eye interrupts the profile of the head, this specimen is *A. stomias*; if the upper eye does not interrupt the profile of the head, the specimen is *A. evermanni*. If the head is in bad shape (e.g., damaged during the trawl operation) or if the examiner has difficulty using eye position and head profile to identify a specimen, the gill arches must be examined. Two or more gill rakers on the upper limb of the second gill arch indicates that the specimen is *A. stomias*; if there is only 1 gill raker, the specimen is *A. evermanni*.

The number of gill rakers on the first gill arch has generally been used to distinguish the two species of *Atheresthes*. However, this study demonstrated a greater overlap between the two species in number of rakers on the first gill arch than the second gill arch (Tables 1, 2), indicating that the second gill arch is a better character for assigning individuals to the species.

The study also suggests that the number of gill rakers on the upper limb of the first gill arch is species specific. If there are 4 or more gill rakers, the specimen is *A. stomias*; 2 or fewer gill rakers indicate the specimen is *A. evermanni*.

The uncertainty in examining the first gill arch is when there are 3 gill rakers on the upper limb. Approximately 25% of *A. stomias* and 50% of *A. evermanni* samples had 3 gill rakers on the upper limb of the first gill arch. Thus, when 3 gill rakers are present on the upper limb of the first gill, the second gill arch must also be examined to distinguish the two species.

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MEI-SUN YANG

Northwest and Alaska Fisheries Center
National Marine Fisheries Service, NOAA
7600 Sand Point Way NE
Seattle, WA 98115-0070

PREDATION OF KARLUK RIVER SOCKEYE SALMON BY COHO SALMON AND CHAR

The number of sockeye salmon, *Oncorhynchus nerka*, in Alaska's Karluk River (Fig. 1) declined from millions to thousands during the early part of the present century. Rounsefell (1958) discussed alternative explanations for the decline including a general loss of fertility of the system as the number of salmon carcasses declined, competition, overfishing, subtle changes in climate, and predation; he concluded that the combined effect of predation and fishing was the most probable explanation. Later, Van Cleave and Bevan (1973) suggested that the weir constructed in the river each year to facilitate counting the fish as they entered the system was the most probable cause of the decline. It prevented free movement of both adults and juveniles in the river. All of these hypotheses remain as potential explanations for the decline.

Fredin et al. (1974) described a relation that showed two equilibrium regions between the spawning stock and the resultant run for sockeye salmon in the Kodiak area. We developed a stock-recruitment curve (Fig. 2) for sockeye salmon in the Karluk River basin that also showed two equilibrium regions, and suggested that the population had "col-

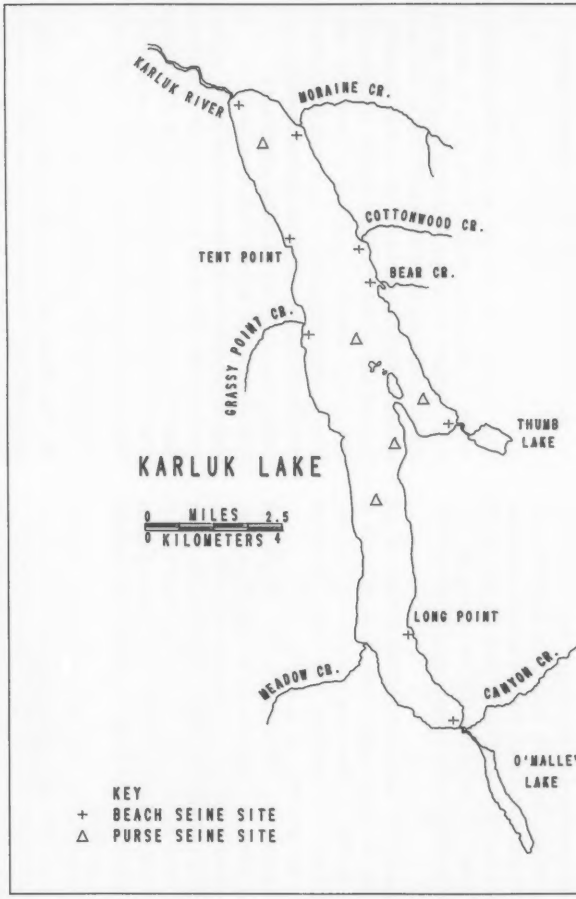
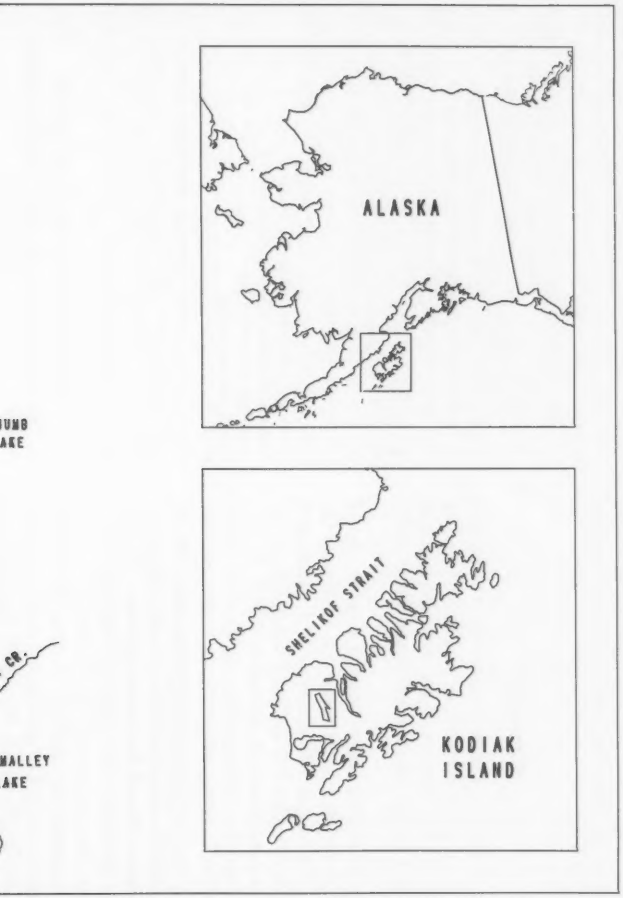


FIGURE 1.—Karluk Lake and associated wat



ed waters, and sampling sites for a predation study.

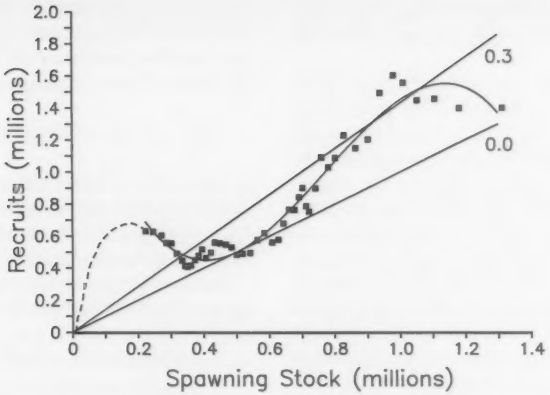


FIGURE 2.—Stock-recruit relation for sockeye salmon in the Karluk River basin. Squares are the running geometric mean (by 9) of stock and recruit estimates for the 1922–77 broods. The curved, solid line was described by $R = 1.83(10^6) + 7.73P + 1.29(10^{-5})P^2 - 5.58(10^{-12})P^3$; where, R = recruits and P = stock. Ages of fish in the escapement (1922–36 from Barnaby 1944; 1937–69 from the Northwest and Alaska Fisheries Center, National Marine Fisheries Service, Auke Bay, AK; 1980–85 from Alaska Department of Fish and Game, Kodiak, AK) were used to estimate the recruits produced by each brood. The diagonal lines show how the replacement line changes as the exploitation rate increases from 0 to 0.3.

lapsed" into the lower of the two. Fishing can cause such a collapse (Peterman 1977) and recovery becomes impossible unless exploitation rates are reduced to levels substantially lower than the rate that caused the collapse.

Multiple equilibria in an exploited population can be caused by depensatory mortality—the loss of a relatively greater fraction of the population when it is small than when it is large (Neave 1953). Several functional responses (Ricker 1954; Holling 1973) have been used to describe relations between prey density and predation rate—one of which (Type III relation) can produce multiple equilibria in the stock-recruitment curve of a prey population (Peterman 1977). The Type III or S-shaped functional response is characteristic of predators that consume a small fraction of the prey at low prey population density; as prey population density increases, however, the predators rapidly increase the fraction consumed through learning or aggregation. The concave, Type II functional response holds when the fraction consumed is high at low prey density.

The apparent potential for stock collapse, as depicted in the Karluk sockeye stock-recruitment curve, could be the consequence of Type III predation mortality. A preliminary survey of the food habits of fish in the system showed that coho salmon, *O. kisutch*, and two chars—the Dolly Varden, *Salvelinus malma*, and Arctic char, *S. alpinus*—were predators of juvenile sockeye salmon. We set out to determine whether the functional responses for coho salmon and for char were of Type II or Type III. Our approach was to describe the relation between the number of prey eaten per predator and the index of prey abundance provided by the annual counts of adult sockeye salmon that entered the system for spawning. Unfortunately, the study had to be terminated after five years because of a management decision to enhance the productivity of Karluk Lake with commercial fertilizer; we could not eliminate the possibility that the effects of fertilization would confound predation responses. We describe the data that were accumulated during five field seasons and our tentative conclusions concerning the role of predation mortality in the dynamics of these sockeye salmon.

Methods

Sampling sites were established at locations around the littoral zone of Karluk Lake at the outlets of spawning streams and at beach spawning areas (Fig. 1) in 1982. The Karluk River was sampled from the outlet at the lake to about 100 m downstream.

In each of the five subsequent years, a field crew sampled each location at weekly intervals, from late April to October.

Juvenile coho salmon were collected with beach seines and minnow traps, and chars with beach seines, floating gill nets, and hook and line. Only coho salmon larger than 80 mm were found to be predators of sockeye salmon during the April–October sampling period. Since char were captured with hook and line or in gill nets, our samples contained only fish that were large enough to consume sockeye salmon fry. Coho salmon were preserved in formalin for examination later, when the contents of the stomachs were removed and the sockeye salmon fry and fingerlings were counted. The chars were tagged and released after the contents were flushed from their stomachs and preserved in formalin.

Results

Juvenile coho salmon were aggregated around tributary outlets and in the littoral areas of Karluk Lake. The chars were found almost exclusively around the tributary outlets and in the Karluk River. Few coho salmon or chars were captured by seining in the pelagic areas of the lake. We did not distinguish between the two chars.

Predation rates for the chars did not increase as the abundance of sockeye salmon increased (Table 1), but the average number of sockeye salmon fry consumed by each coho salmon did increase and appeared to be depensatory (Fig. 3). A general equation (Real 1979) was used to describe the relation between the predation rate (Y) by coho salmon and the index of prey abundance (X),

$$Y = bX^c/(1 + aX^c). \quad (1)$$

A value of $c = 1$ provides a classic, Type II functional response curve, while values of c exceeding 1.0 provide a sigmoid, depensatory shape. A value of $c = 2$ gives the classic Type III curve.

Best (least squares) fit values for a, b, and c were obtained by transforming Equation (1) into the form

$$\ln(1/Y - a/b) = \ln(b^{-1}) - c\ln(X). \quad (2)$$

Using trial values of a/b, we regressed the left side of Equation (2) on $\ln X$ until we identified the value of a/b giving the lowest residual variance. The

TABLE 1.—Predation on juvenile sockeye salmon by predatory coho salmon (i.e., juvenile coho salmon longer than 80 mm) and chars in Karluk Lake, AK during June and July from 1982 to 1986.

	Coho salmon		Chars		Sockeye
Year	Number examined	Predation rate	Number examined	Predation rate	salmon escapement
1982	252	0.475	—	—	220,000
1983	3,132	0.076	95	0.98	164,000
1984	250	0.661	128	19.45	436,000
1985	956	0.452	485	10.06	420,000
1986	423	0.740	571	4.50	996,000

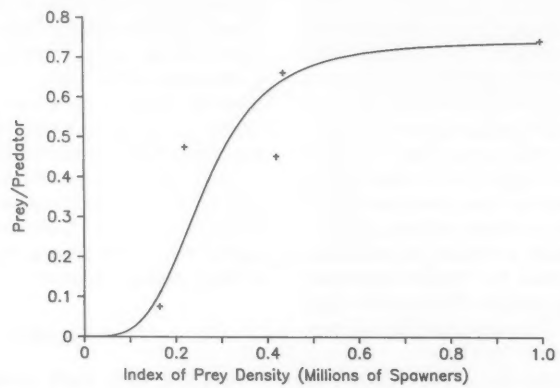


FIGURE 3.—Functional response curve for coho salmon greater than 80 mm (predators) and sockeye salmon (prey) in Karluk Lake. The index of prey abundance was divided by 1,000,000 (e.g. index 0.8 = 800,000 adults in the escapement).

results are $a/b = 1.35$, $c = 3.74$ (standard error = 0.79), $R^2 = 0.88$, $\ln(b^{-1}) = 46.98$.

Hence Equation (1) becomes

$$Y = bX^{3.74}/(1 + 1.35bX^{3.74}) : b = e^{-46.98}.$$

Inasmuch as Y ranges between zero and b/a, it seems unlikely that Y, or a corresponding statistical error term for Equation (1) would be approximated by a normal distribution. On the other hand, so long as Y does not rise above b/a (to which Equation (1) constrains it), the left side of Equation (2) lies between $-\infty$ and $+\infty$, and the error term is more likely approximated by a normal distribution. Consequently, we cautiously used the standard error associated with c, to test whether $c > 1.0$; that is, whether the functional response curve is sigmoid (Type III). In fact, c lies more than 3.5 standard errors above 1 (Type II response) and more than 2.2 standard errors above 2 (Type III response). Although the power of a test involving only 5 data points is weak, we feel that a tentative conclusion of depensatory predation by juvenile coho salmon is justified.

Discussion

Many adult salmon as they attempt to get to the spawning grounds, and as they spawn, are killed by Kodiak brown bears. Gard (1971) reviewed the available literature concerning predation of salmon by bears at Karluk and, in years when fish were not abundant, noted that bears had been observed to leave the salmon spawning areas to feed on berries in the local area, indicating that their predation also may be depensatory. We used data from Gard's summary to approximate the relation between the number of adult sockeye salmon in a run (X) and the number of unspawned adults (Y) estimated to have been killed by bears (Fig. 4). Although R^2 was only 0.424, a depensatory relation was indicated as $Y = X^{2.106}/(3102.85 + 0.00435X^{2.106})$; c, from Equation (1), was 2.106, with a standard error of 1.098. Because predation of sockeye salmon by bears, as well as predation by coho salmon, appeared to be depensatory, it is unlikely that predation by coho salmon alone was the sole cause of the complex stock-recruitment curve for sockeye salmon.

Prudent management of these salmon, and of salmon in systems similar to Karluk, may require regulation of harvest to prevent collapse of populations into relatively low equilibrium regions. Harvest levels that would have prevented collapse of the Karluk population can be estimated from the stock-recruitment curve (Fig. 2). An exploitation rate between 30 and 35% of the recruits should have maintained stock sizes associated with the upper equilibrium region. Exploitation at a constant rate of 0.40 increases the slope of the replacement line to the point that collapse of the population into the lower equilibrium region becomes inevitable (see Peterman 1977 for a description of the relation between the size of stability regions and exploitation rate). When depensatory mortality is potentially high for economically important populations, it may be necessary to limit exploitation to less than 35% of the recruits to prevent collapse.

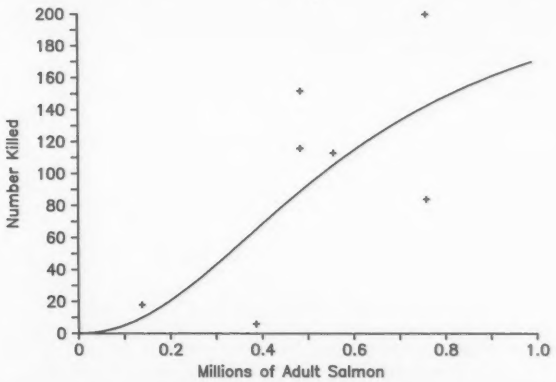


FIGURE 4.—Functional response curve for predation of sockeye salmon by bears. Number killed is thousands of unspawned salmon.

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JOHN D. MCINTYRE
REGINALD R. REISENBICHLER
JOHN M. EMLEN

National Fishery Research Center
U.S. Fish and Wildlife Service
Building 204, Naval Station
Seattle, WA 98115

RICHARD L. WILMOT
JAMES E. FINN

National Fish and Wildlife Research Center
U.S. Fish and Wildlife Service
1101 E. Tudor Road
Anchorage, AK 99503

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